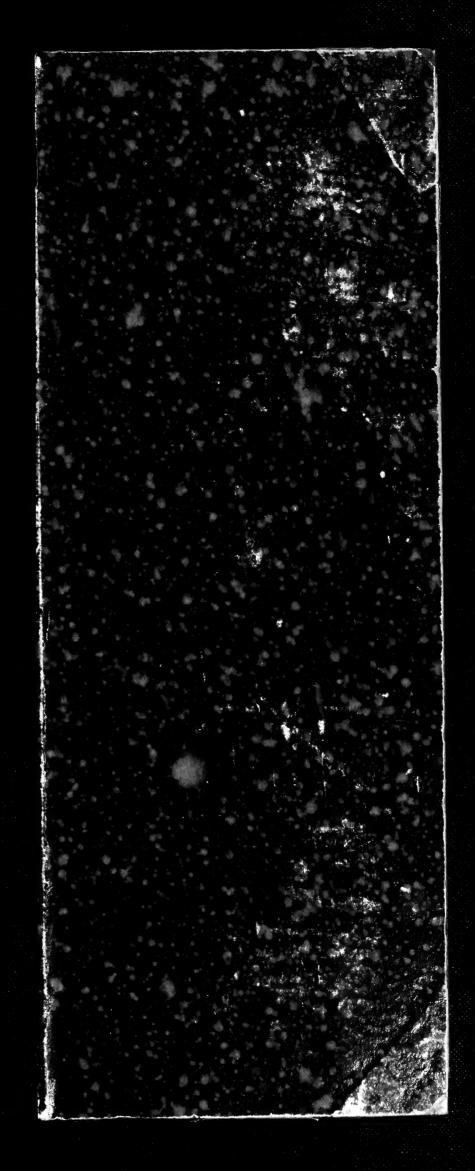
WASHINGTON

The Homology of the Mouth-Parts of Insect Larvae

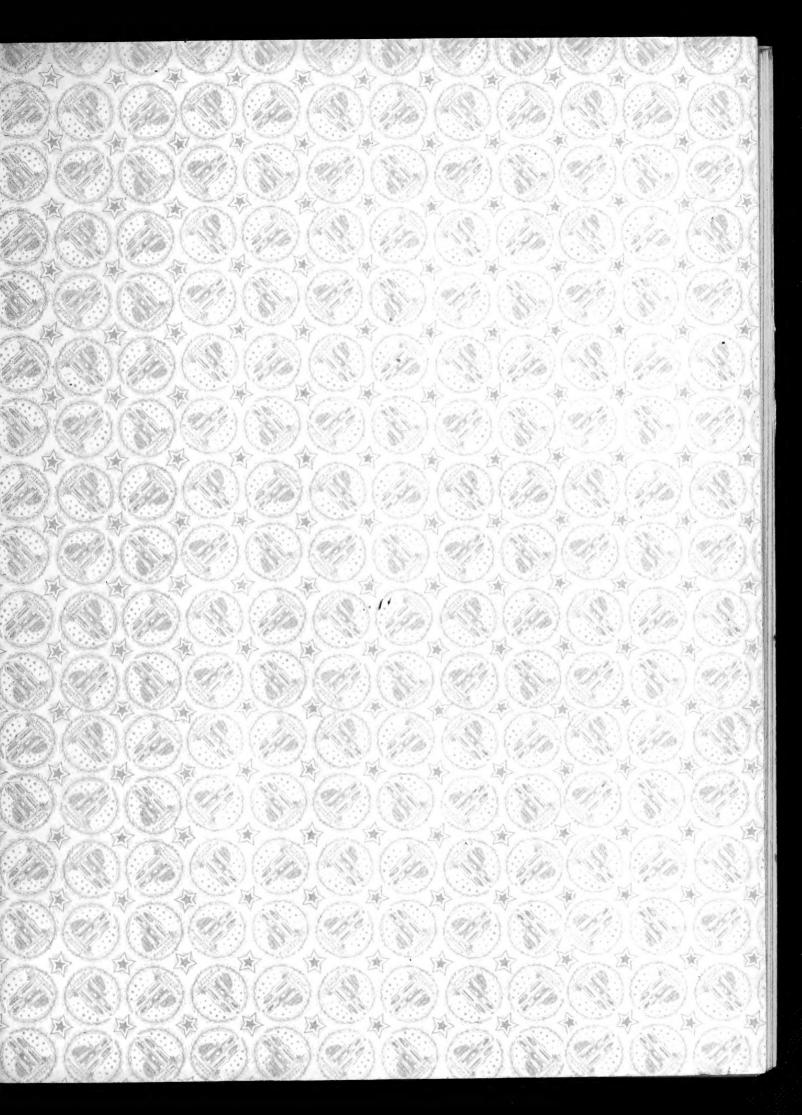
Entomology

A. M.

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THE HOMOLOGY OF THE MOUTH-PARTS OF INSECT LARVAE

BY

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A. B. Smith College, 1912

THESIS

Submitted in Partial Fulfillment of the Requirements for the

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I. INTRODUCTION

Crustaceans and insects have probably been evolved from some common segmented arthropod ancestor with a pair of appendages on each segment. This typical appendage, according to Boas, was probably composed of the following parts: A basal stalk or protopodite, composed of a coxopodite and a basipodite, and three parts borne at the distal margin of the basipodite. These are, a segmented endopodite, an exopodite, and a lamella-like epipodite.

This typical ancestral appendage has been least modified in the maxillipedes of the crustaceans, also the first and second maxillae of such forms as the lobster and crayfish approach near to the probable ancestral type.

In insects, the most highly specialized arthropods, the mouth-parts and antennae have been greatly modified, although they are the homologues of a typical appendage. The antennae are composed of protopodite and endopodite. The mandibles, according to most authors, represent only the protopodite, the terminal parts having been entirely atrophied. The maxillae and labium show a nearer approach to the primitive condition. The cardo and submentum represent the coxopodite. The basipodite is homologous with the stipes or one-half the mentum, the exopodite with the maxillary or labial palpus, the endopodite with the inner lobe of the labium or maxilla, which is split to form the glossa and paraglossa or the galea and



lacinia.

There are in insects all grades of specialization and modification of generalized mouth-parts, and the homologies of these parts offer most interesting and intricate problems to the student of insect morphology.

HOMOLOGY AND METAMORPHOSIS

There has been an enormous amount of work done on the homologies of the mouth-parts of insects, but this has been confined largely to the study of adults. In the specialized metabolous orders where there has been such a high degree of specialization and where there is such a difference between the larval and adult forms, the problem of homologies of larval mouth-parts has been neglected. These homologies may be of value in three respects.

In the first place, the practical importance of these homologies may be touched upon. There is little known about the classification of immature forms, particularly where these forms are very different from adults, as in those orders with a complete metamorphosis. Furthermore, there can be no adequate classification of immature insects until the homologies of the parts are worked out and there is some morphological basis for the construction of analytical tables. The mouthparts with other parts must be homologized in preparation for all systematic work. This investigation is the result of an attempt to homologize the mouth-parts of insect larvae.

In the second place, there has been no cognizance taken



of the evidence of larval conditions that is available in determining homologies of adults. This work has been done entirely on adults by the study of the comparative morphology of different forms. In every other branch of biology the study of the homologies of parts is aided by the study of the ontogeny of the individual in question as well as by comparative morphology. Neither of these methods is complete by itself, nor can the results from either method along be conclusive. Embryology and comparative morphology should go hand in hand. The latter field has been covered by many investigators, but the former, interpreting embryology as the study of the changes in an individual from the time of the fertilized egg until the mature form is produced, remains practically untouched. According to this definition, which is authorized by Professor H. H. Wilder, the larva is but an embryonic stage of the imago. The condition of the parts of a larva is therefore embryonic and necessarily more generalized than the conditions found in the adult. The difficult has been that workers observing the great differences in the structure of imaginal and larval forms and over-emphasizing these differences have failed to take into account the fact that the imaginal organs are the homologues of the larval organs and have been developed from them. There are many modifications and specializations of larval organs resulting from the necessity of structural adaptation to external conditions. These modifications are often so striking and the departure from the gen-



eralized adult type so great that it is difficult and often impossible to homologize the structures with those of a generalized insect and to determine what parts have been modified, by comparison of adult forms alone. It is at this point that the value of the study of larval forms may be seen. Since the larva is an earlier ontogenetic condition, the parts may be more easily homologized, and the determinations may be of great value in the interpretation of the more specialized adults, for in general the parts that are well developed in the larva will be present, though greatly modified, in the adult. It is true, however, that in some cases larval parts atrophy entirely before maturity is reached, and are entirely wanting in the adult, but there are rarely parts in the image that are not present in the larva.

As correct determination of the homologies of the mouthparts is a factor in ascertaining the phylogeny of different forms, study of the larvae will help in establishing a more perfect system of phylogenies.

In the third place, the study of larval forms may do much to ascertain the meaning of metamorphosis. The changes in form during metamorphosis have always been over-emphasized, and with the acceptance of these striking outward changes there has been no effort to find the similarities and likenesses in details of structure. The pupal stage during which the larva undergoes metamorphosis may be considered according to our definition as the last stage in the embryonic development



of the individual. It is a period of rapid change, development, and further differentiation, features that are characteristic of all embryonic life. These rapid changes are in preparation for the life of the adult. These phenomena are not peculiar to metamorphic forms, but are common to the development of all organisms. It cannot be stated with too great emphasis that in all forms there is a radical change in the form, size, appearance and function of organs during embryonic life and that there is no particular meaning attached to these changes further than the application of the law of biogenesis, that the life history of the individual repeats the life history of the race. The truth is that in the great majority of cases all these changes in the ontogeny of insects take place after birth, and, as maturity is not reached until comparatively late in the life history of the individual, many of them late in life. Moreover, the change in the form and mode of life between the highly specialized metabolous insects and their primitive wingless ancestors has been great. Wings have been evolved in the history of the race, the mode of life has been changed and as a result the structure and the form of the thoracic sclerites and their musculature have been modified in adaptation to aerial, as opposed to terrestrial, life. It must be stated again with emphasis that the path which the race has followed will be retraced largely by the individual in the course of its development, and that the changes that have occurred in racial evolution will be undergone, in the major-



are so great that for the individual to undergo them during active life would unfit it for the pursuance of its ordinary life habits. Transitional forms in the evolution of a race are weak, and survive but a short time, and such forms would be of disadvantage in the case of an individual, serving to lessen its chances of survival in the struggle for existence.

To obviate this difficulty the most radical processes of modification are crowded into as short a period of time as possible so that the transition stage may be of short duration. During this time the ordinary habits of life are abandoned and the entire organism given over to the processes of development. A large food supply is stored up during the larval life of the individual which can be used in these processes, as of necessity during such a period a large amount of nourishment is needed.

Thus, while the processes which occur during metamorphosis are truly embryonic and primary in origin there has been a secondary specialization in the life of the individual in the manner in which they are undergone, to ameliorate the disadvantages of transitional stages which are necessitated by radical modifications of structure.

Attention may be called to the fact that there is no absolute dividing line between the so-called metabolous and ametabolous orders, the difference between them is one of degree and not of kind. In all orders there is a gradual change



from the larval structure to that found in the adult. In the most primitive forms this difference is slight, and in some forms is discernible only by means of sections. As the forms depart farther and farther from the primitive type the differences between the adult and immature forms are greater and greater, until, in the highly specialized orders, there is no superficial resemblance between the two stages. But the forms where the difference is slight undergo as true a metamorphosis as the specialized forms.

The adult grasshopper is not like the first nymphal stage, and there is a gradual metamorphosis between the hatching of the egg and the completion of the mature form. In this instance the habits of the adult are not so different from the habits of the primitive terrestrial forms as in the more specialized orders, with the result that the modifications can take place more gradually without interferring with the ordinary life habits of the individual. In the more specialezed forms, where the mode of life has become more perfectly aerial, the modifications are greater, and take place more rapidly during a resting stage—but in all cases they are the same kind of processes, modifications of existing parts to fit the adult individual for the life it leads.

If the fundamental similarities can be pointed out between the larva and the adult, and the differences not so emphasized, the fact that metamorphosis is not any strange phenomenon with special significance but simply a phase of the embryonic life



of the individual, may be accepted.

PREVIOUS INVESTIGATIONS

mouth-parts is extremely scanty. The only important paper definitely devoted to the subject is that by Professor Kellog on "The Development and Homologies of the Mouth-Parts of Insects", published in the American Naturalist in 1902. In this paper Professor Kellog covers all the metabolous orders, but in a very superficial and unsatisfactory manner. There is no attention paid to the head sclerites, and many of the details of morphology are ignored. He emphasizes the value of the study of the ontogenetic development of mouthparts, but deals entirely in generalities, and seems to have written from one point of view, a corroboration of his own homologies of adult dipterous mouth-parts.

Professor Carpenter and Miss MacDowell published a paper in the Quarterly Journal of Microscopic Science in 1912 in which the mouth-parts of some beetle larvae are described in great detail. There is no consideration taken of the head capsule in the determination of the homologies.

The work done in this field consists largely of scattered observations with no connection between them. These isolated facts are of little value in a comprehensive study of the subject.

SCOPE OF THE INVESTIGATION

It is impossible to work on the mouth-parts and to de-



termine the homologies with any degree of accuracy by confining the study to mouth-parts alone. They cannot be isolated and considered as an entity for they are a part of a whole and the rest of that whole must be given due consideration. It is necessary, then, to study the fixed parts of the head, for it is their form, position and direction which are important factors in determining the shapes, relative positions and lines of modification of the mouth-parts. The head sclerites are of great value in determining the sclerites of the buccal parts.

The internal skeleton or tentorium is included in the fixed parts of the head, and indeed it is always intimately associated with the mouth-parts and often furnishes points of articulation for them.

This necessity for study of the fixed parts is now obvious, and the parts of the head capsule will, in each form studied, be considered before the question of the homologies of the mouth-parts is touched upon.

When such a comparison is possible, it is advisable to make use of the advantages and assistance offered by the study of adult forms.

METHODS

In all forms the heads were soaked in a ten percent. solution of caustic potash for at least twenty-four hours. This serves to disentegrate the muscle masses, softens the chitin and removes some of the pigment. After soaking in caustic potash, the specimens were washed and put in seventy per cent.



alcohol. Some were studied in alcohol, others after dehydration were cleared and studied in carbol-xylene.

were in all cases studied under a binocular microscope, largely by means of dissection, as it was found that the relationship of the parts was more easily discovered if the specimens were in a natural position. In cases where the specimens were small or some point difficult to determine, parts of the head were mounted on slides.

TENTORIUM: - Preparations for the study of the internal skeleton were made by halving the head by a dorso-central cut on the meson or by a cut perpendicular to the meson and parallel to and near the fronto-clypeal suture. In some cases the caudal and cephalic ends and part of the lateral aspects were cut off so that the entire tentorium was visible. These preparations were cut before the specimens were put in caustic potash, as the masses of muscle prevented the tearing or breaking of the chitinous parts. After soaking in ten per cent. caustic potash, the specimens were hardened in alcohol and cleared. Total heads were used for comparison.

MOVABLE PARTS OF THE HEAD: The mouth-parts were in all cases studied "in situ" before mounted preparations were made, in order that the interrelationships might be known before an attempt was made to homologize the parts.

MANDIBLES:-Where the specimens were small the mandibles were cleared and mounted in balsam. When large, they were



studied entirely under the binocular. In all cases articulations were determined by dissection under the microscope.

MAXILLAE:- The position, connections, and articulations of the maxillae were studied in the same way. Two mounted preparations of each maxilla were made, one with the ectal, one with the ental surface uppermost. In cases where the maxillae were not free but united with the labium or gula, entire mounts of the connected parts were made.

LABIUM: - The labium was studied in the same way as the maxillae. When it was fused with the maxillae, the parts were studied together.

PROPHARYNX AND HYPOPHARYNX:- Before the heads were soaked in potash the lateral aspects of the heads were cut for their entire length. After the muscles had been disintegrated by soaking in dilute caustic potash, the entire pharynx with the propharynx and hypopharynx attached could be removed by pulling gently, and cutting away chitinous parts that were closely associated. Mounted preparations were made of this. In the more highly specialized forms where there is a greater development of the hypopharynx and a more intricate relationship between it and the labium and the maxillae, flat mounts are inadequate and must be supplemented by a careful study of the parts "in situ".

SALIVARY DUCTS: - In the more generalized forms the ducts of the functional salivary glands open into the mouth cavity through the lingua and furnish important evidence in deter-



mining this part of the hypopharynx. In some cases this opening is not clear in mounted preparations. In order to ascertain with accuracy the positions of the openings of the ducts, the ducts were dissected out for their entire length. This was done by opening the specimens on the meson of the venter, pinning them flat in a small dissecting pan, and tracing the ducts from the salivary glands to their external openings. In the Lepidoptera the same method was pursued with the silk ducts and the functional salivary glands.

II. CORYDALIS CORNUTUS

Corydalis is a neuropteron which represents the most generalized condition found in insects having a complete metamorphosis. The mouth-parts are suited for biting in the adult as well as in the larva. It is for these reasons that this form has been chosen as the basis of comparison for other less generalized forms.

THE FIXED PARTS OF THE HEAD

The fixed parts of the head comprise the head capsule or external skeleton and the tentorium, the internal skeleton, which supports not only the head capsule but the internal organs of the head, and furnishes support for some of the mouthparts. The parts of the head capsule will be considered first.

Epicranial Suture: (Pl. I):- The mouth-opening is directed cephalad, and the epicranial suture extends from the caudal margin of the head to the mesal margins of the antennal sockets.

It proceeds one-half the entire length of the head directly



cephalad on the meson where it divides. The two arms extend laterad, turn cephalad abruptly and then again laterad to the antennal sockets.

Occiput (P1.I):- At the caudal end of the dorsal aspect there is a prominent semi-circular piece divided into two equal parts by the stem of the epicranial suture. This piece, which is the occiput, is confined entirely to the dorsal aspect and projects caudad of the margin of the lateral and ventral aspects of the head.

Vertex (Pl. I):- The greater part of the dorsal aspect is occupied by the vertex which is that part cephalad of the occiput and laterad of the epicranial suture. It extends on each side from the occiput to the cephalic margin of the head capsule. near the point of insertion of the antenna, and from the epicranial suture around to the lateral aspect of the head where it is fused with the gena for its entire length without any indication of a suture. The ocularium, the region on each side of the vertex bearing the simple eyes, is located for the most part on the dorso-lateral angle of the vertex, although it is only entirely apparent from a lateral aspect. On the ocularium are six, rarely seven, simple eyes, five of which are arranged about a central one. There is a prominent transverse ridge just caudad of the ocularium and another on the lateral aspect of the head between the caudad margin of the vertex and the ocularium. Both of these ridges extend for a short distance only onto the dorsal and ventral aspects of



the head.

caudal and lateral margins by the arms of the epicranial suture. These arms extend from the meson cephalo-laterad, turn cephalad and then turn abdruptly laterad. At this second angle the anterior arms of the tentorium are invaginated and these points mark the cephalic extent of the front. The fronto-clypeal suture, which extends between the invaginations of the anterior arms of the tentorium and which marks the line of separation between the clypeus and front and which is present in most generalized insects, is obsolete and the front fused with the sclerite cephalad of it, the first clypeus. The front is a small sclerite. It is about three times as wide as long, and one-fourth the length of the vertex, and one-half of its width.

The First Clypeus (Pl. I):- The first clypeus is cephalad of the front and is completely fused with it, but is separated from the sclerite laterad of it by a distinct suture extending from the invaginations of the anterior arms of the tentorium cephalad to the margin of the head, and also is separated from the sclerite cephalad of it by a transverse suture extending between the distal ends of these two longitudinal sutures. The first clypeus is rectangular in shape, being of the same length and width as the front and three times as broad as long. There is a short, broad swelling on the cephalic margin.

The Second Clypeus(Pl. I):- The second clypeus, the scler-



nated by writers as the clypeus, is separated from it by the transverse suture between the latero-distal angles of the first clypeus. It is not quite as long as the first clypeus. The proximal margin is as wide as the first clypeus, but the lateral margins converge so that the distal margin is only two-thirds as wide as the proximal. The proximal angles are, therefore, decidedly acute, with the distal angles obtuse. In all but the most generalized forms, the suture between the first and second clypeus is obsolete, so that these two sclerites are fused to form what may be termed simply the clypeus.

Labrum (Pl. I):- The labrum is the long, narrow flap borne at the cephalic end of the second clypeus. This is narrower and longer than the second clypeus. Near its distal end the lateral margins converge to form a roundly pointed distal margin. On each side where the lateral margins converge there is a pair of long pointed setae with a pair of short, fine setae just caudad of them. The cephalic margin of the clypeus is shallowly emarginate on the meson.

Antecoxal Piece of the Mandible (Pls. I and III):- Laterad of the first clypeus and separated from it by the suture extending from the invagination of the anterior arms of the tentorium to the margin of the head and separated from the front by the arm of the epicranial suture there is a small, somewhat triangular sclerite extending to the antennal socket. The mandible is articulated with it, and it is called by Com-



stock and Kochi the antecoxal piece of the mandible.

In a typical thoracic leg the coxa is articulated in two places—one is a pleural, the other a ventral articulation.

The pleural articulation is against a coxal process. This process is at the ventral end of the pleural suture, which is between the episternum and the epimeron, and along which the entopleuron is invaginated. The coxal process is formed by a swelling at the ventral end of the entopleuron. The ventral articulation is against a small condyle at the posterior end of a small sclerite which extends caudad from the anterior angle of the episternum along the lateral margin of the sternellum. This Professor Comstock calls the antecoxal piece, and Dr. MacGillivray the anterior trochantin. The small triangular sclerite laterad of the clypeus is the homologue of this, as the mandible articulates against and is termed by Professor Comstock the antecoxal piece of the mandible.

As the mandibles are the appendages of the postgenal segment, Comstock explains the position of the antecoxal pieces which must be part of the postgenal segment by the dorsal flexure of the procephalon and the consolidation of the segments of the head, in which processes the antecoxal piece has been pushed out of the postgenal segment past the labrum to a position laterad of the clypeus.

In all but the most generalized forms the suture separating the antecoxal piece from the first clypeus are wanting, so that the mandible apparently articulates directly against



the clypeus, which is in reality made up of four parts, two central pieces, a frist and second clypeus, and two lateral sclerites, the antecoxal pieces. In the adult Corydalis the antecoxal pieces are fused with the first clypeus.

In the typical thoracic appendage there is a sclerite lying between the antecoxal piece and the coxa except at the mesal end, where the coxa articulates against the antecoxal piece. The sclerite lying between the coxa and the antecoxal piece is not articulated with the coxa, but lies between the points of articulation. Comstock calls this simply the trochantin, and MacGillivray the posterior trochantin. In a few of the more generalized forms, the homologue of this sclerite is present in the head in the shape of a small, usually crescentshaped piece on each side lying between the dorsal and ventral articulations of the mandible and separating the mandible from the head capsule. Such a sclerite is never found in forms in which the antecoxal piece is distinct. This sclerite is called by Comstock the trochantin of the mandible. According to the terminology of MacGillivray, it would be the posterior trochantin of the mandible.

Gula (Pl. II):- The median, inverted, T-shaped sclerite on the meson of the venter extending from the caudal to the cephalic margin of the head is the gula. Near it's distal end it widens out to form a broad band, the gular bar. From the angle where it begins to broaden, in which the invaginations of the posterior arms of the tentorium are seen as dis-



tinct pits, the sutures on the caudal margin extend distolaterad to the margin of the head. On its cephalic margin the bar of the gula is deeply concave, the submentum fitting into this concavity.

genae (Pls. II and III):- The area occupying the larger part of the ventral aspect of the head and extending on each side between the gula and the vertex is the gena. It extends on the caudal end from a small crescent-shaped sclerite on the lateral aspect of the head at the margin of the occipital foramen to a small sclerite on the cephalic margin of the head, the postgena.

Postgenae (Pl. II):- The postgenae are the small sclerites located cephalad of the genae and laterad of the gular bar. Each postgena lies on the distal margin of the head capsule. Each is separated from the gena by a curving suture extending from near the distal end of the gular sutures to the margin of the head, ventrad of the ocularium. The postgenae themselves extend mesad, under the gular bar where they have deep acetabula for the articulation of the maxillae.

Microthorax (Pls. I, II and III):- Directly caudad of the gula there is a small square sclerite which is one of the ventral cervical sclerites, the sternellum of the labial segment. The seventh head segment, according to Professor Comstock, is the labial segment; it has for its sclerites all the cervical sclerites. The gula is homologous with the anterior sclerite of the sternum, which is composed in all the thoracic segments



typically of two parts. The labrum, which is composed of two fused appendages, represents the appendages of the microthoracic segment. Packard homologizes this small sclerite at the base of the gula in Corydalis with the occiput, and in his sixth and last head segment he makes the occiput the only sclerite and calls the gula part of the appendages of that segment. In general, that homology may be criticized on the ground that all the parts of a typical appendage are present in the labium itself and the gula cannot be homologized with any part of a typical appendage. The homology of Comstock is correct, it seems. Moreover, if this sclerite at the base of the gula is the occiput, what is the large dorsal semicircular sclerite and the lateral crescent-shaped sclerite extending between the two? To make this interpretation possible, it necessitates the dorsal sclerites being part of the tergum of the microthorax. This is impossible, as will be shown later.

There is a crescent-shaped piece extending from the angle between the gula and the sternum of the labial segment around the lateral aspect of the head to the lateral margin of the occiput. This cannot be interpreted as anything but one of the cervical pleural sclerites.

A short way cephalad of the occiput there is a suture which extends from the lateral margin of the gula at its caudal end and onto the dorsal aspect of the head where it soon becomes obsolete. This suture is probably secondary in origin, for if homologized with the occipital suture, it would



necessitate calling the region immediately caudad of it the occiput and the large semi-circle at the caudal margin the tergal cervical sclerite. This is practically out of the question, for this piece is divided by the epicranial suture. The epicranial suture is a remnant of the dorsal line of closure in the embryo, and it is not probable that this line of closure would be so clearly indicated in the tergum of the nect when it is not apparent at all in the thorax. In the Orthoptera, also, the occiput is crossed by the epicranial suture, a condition typical of generalized forms. If this dorsal piece cannot be anything but the occiput and the lateral sclerite a pleurite of the microthorax, the sclerite at the caudal end of the gula must be one of the sternal sclerites of the microthorax. Professor Comstock goes so far as to identify it with the posterior sclerite or sternellum of the cervical segment, saying that the gula is the homologue of the anterior segment of the sternum, the sternannum. From the evidence of the condition of the gula in a carabid larva, it seems more probable that the connecting membrane of the neck has been pulled forward to fill the gap between the occipital foramen and the labium, and that this membrane has been secondarily chitinized and incorporated as part of the head capsule, rather than that a definite sclerite has been drawn forward.

The only logical interpretation of these parts is to call the dorsal piece the occiput, the caudo-lateral piece a cer-



vical pleurite, with the suture cephalad of this a secondary one, and the caudo-ventral sclerite one of the sternal sclerites of the labial segment.

TENTORIUM: (Pls. IV and V):- The tentorium also shows a generalized condition in this form.

Anterior Arms (Pl. IV):- The anterior arms are invaginated on each side in the angle between the front, clypeus, vertex, and antecoxal piece of the mandible. From this point each arm proceeds ventrad through the head cavity as a slender pillar. which fuses with one of the posterior arms of the tentorium at the point of invagination.

Posterior Arms (Pls. IV and V):- The posterior arms are invaginated in the angles between the gular bar and stem of the inverted T of the gula. These openings are very noticeable on the ventral side as long slits. Each of the posterior arms has a short free caudal extension along each gular suture and a flange-like extension latero-distad along this suture. There is no indication of either a frontal plate or a body of the tentorium, which are results of mesal extensions of the anterior arms, in the case of the former, and the posterior arms in the case of the latter, fusing on the meson.

Dorsal Arms (Pls. IV and V):- The dorsal arms are invaginated on the lateral aspects between the ocularium and the antennal socket. Each one proceeds mesad along the epicranial suture, between the vertex and the antecoxal piece of the mandible, to the invagination of the anterior arm. The dorsal



arm is closely applied to the head capsule for its entire length.

The condition found in the adult Corydalis is practically the same. The caudal extensions of the posterior arms are longer and from each anterior arm there is a short mesal projection along the line where the front and clypeus are fused. These indicate the development of a frontal plate in less generalized forms. It is interesting to note that this is a more primitive condition than that found in even Periplaneta or in Melanoplus. In both of these species a frontal plate and a body of the tentorium have been developed from extensions of the anterior and posterior arms, while in Corydalis we find the three essential invaginations, but in a more simple relationship.

MOVABLE PARTS OF THE HEAD

The movable parts of the head which will be considered are the mandibles, maxillae, labium, propharynx, and hypopharynx. The antennae will not be described, as they are of no value in determining the homologies of other parts of the head.

MANDIBLES (Pl. VI):- The mandibles of Corydalis are long, strong, and very heavily chitinized. They are convex on the dorsal side and concave on the ventral. Each mandible is triangular in cross-section, there being two lateral edges, while the dorsal and ventral sides meet in a single mesal edge. The distal third of the mesal margin is produced into four strong teeth, the most distal being the largest and shaped



somewhat like a scimitar. On the latero-dorsal angle there is an acetabulum which is on a projection and into which fits a condyle on the lateral margin of the antecoxal piece. On the latero-ventral angle there is a very long, heavy condyle which fits into a deep acetabulum in the postgena. Each mandible is also connected with the maxilla by a strong membrane which attaches to the cardo and to a depression on the proximal half of the stipes on the dorsal side, and to the mesal angle of the mandible.

The mandibles are of the same shape in the adult female, with the same articulations, but instead of being strong and heavily chitinized, are soft with little chitin except at points of articulation with the head capsule.

MAXILLAE (Pls. VII and VIII):- The maxillae of Corydalis are generally rectangular in shape and are attached to the postgenae in deep acetabula dorsad of the gula. This form of articulation is the same as that found in an adult Harpalus, the articulation being in both instances concealed by the overlapping gula.

Cardo (P1. VIII):- The cardo, the proximal sclerite of the maxilla, is heart-shaped, the apex of the heart being at the proximal end and forming the condyle which fits into the deep invagination of the postgena. Unlike the condyles of the mandibles, this condyle is not chitinized. It is simply a projection which fits into the postgena. This is not a stable type of articulation, and to prevent the maxilla slipping out



of place, on the dorsal side there is a chitinized flange just caudad of the acetabulum of the postgena. If the maxilla should tend to slip too far one way or the other, this ridge would catch on either edge of the postgena and hold it in place. The entire cardo is slightly globular on the ventral aspect, but concave on the dorsal. It is articulated with the distal portion of the maxilla only at its disto-lateral angle, which has a slightly chitinized projection fitting over the distal part of the maxilla.

Stipes (Pls. VII and VIII):- The distal part of the maxilla is rectangular in shape from the ventral aspect, and has at its distal end two segmented appendages. The maxilla is hollow and near the distal end narrows to a membranous portion which bears two appendages. Normally this part is retracted within the cylinder so far that only the tip ends of the appendages are visible beyond the distal margin. However, if these be pulled out carefully, the true relation of the parts and the entire extent of the appendages may be observed. The stipes occupies nearly all of the distal part of the maxilla. It's lateral margin is slightly more chitinized and setaceous. At each angle where the stipes narrows there is a bundle of very long setae. The membranous part is also covered with minute triangular papillae.

Palpifer (Pl. VIII):- The palpifer is a sclerite located cephalad of the lateral half of the distal end of the stipes.

It appears to be the proximal segment of the maxillary palpus.



It is pentagonal in out-line, and bears at the lateral angle two long setae.

Maxillary Palpus (Pl. VIII):- The four-segmented appendage attached to the palpifer is the maxillary palpus. The first three segments are sub-equal in length, being successively narrower from the proximal to the distal end. The distal segment is very short and narrow. The entire palpus is glabrous.

Galea (P1. VIII):- The galea is the two-segmented appendage cephalad of the mesal half of the stipes. The first segment is slightly longer than the second and has a ring of short setae around its distal margin. The second segment is narrower and truncate at the tip.

Lacinia (Pl. VII):- On the mesal margin of the stipes extending from the cardo cephalad to the point where the stipes narrows there is a long, heavily chitinized piece. There is no definite suture between the stipes and this piece, but the line of fusion is distinct. The entire piece is setaceous, and along its mesal margin there is a regularly arranged row of long, heavy setae. The distal end of this piece is produced into a very slight projection. The entire piece is the homologue of the galea. In the adult the whole maxilla is shortened, the lacinia is densely setaceous, and the minute projection characteristic of the larva is developed into a prominent free projection one-third the length of the maxilla.

LABIUM (Pl. IX): - The labium is the large lower lip, which



on the ventral aspect of the head, mesad of the maxillae. The sclerites of a typical labium are all fairly distinct.

Submentum (Pl. IX):- The submentum, the proximal sclerite of the labium, is fitted into the deep concavity on the cephalic margin of the gular bar. It is the largest sclerite of the labium and is oval in out-line, the cephalic half being rounded to fit the proximal margin of the mentum. The caudal half of the submentum is chitinized and covered with short, thick, heavy setae. The distal half is hyaline and glabrous.

Mentum (Pl. IX):- The mentum, which is a small, inconspicuous sclerite cephalad of the submentum, consists of a narrow band curving on each side from the middle of the lateral margin of the submentum to the meson. In the adult the submentum extends cephalad over the mentum, which is visible only on the lateral margins.

Ligula (Pl. IX):- The ligula in Corydalis is large, being about equal in size to the submentum. It is composed of the following parts:

Palpigers (Pl. IX):- The palpigers are prominent, shoul; der-like processes on the lateral margins of the ligula which bear the labial palpi at their distal margins. They extend caudad, laterad of the mentum, to near the middle of the lateral margin of the submentum. They are not setaceous, except for a few short setae at the attachment of the labial palpi.

Labial Palpi (Pl. IX): - Each labial palpus is three-segmented, and is attached on the lateral margin of the ligula



to the distal end of the palpiger. The proximal segment has a row of setae on the mesal surface and also a row of setae around it's distal margin. The two distal segments are glabrous. The last segment is truncate, and bears a few tiny organs of special sense on it's distal end.

Paraglossae (Pl. IX):- The paraglossae are the large lobes comprising the greater part of the ligula. The distal half of the paraglossae is covered with setae which vary considerably in size.

Glossae (P1. IX):- There is a slender, median, pendantshaped lobe lying ventrad of the paraglossae. This is not
separated from the paraglossae by a definite suture, but is
quite distinct as it is more heavily chitinized than the paraglossae and glabrous, while the paraglossae are densely setaceous. It is probable that this small part represents the
greatly reduced and fused glossae. Professor Kellog, in his
preliminary paper on the mouth-parts of insects, says that the
paraglossae are entirely wanting and that the large terminal
lobes are the glossae. This interpretation seems improbable,
as in most cases where either are reduced it is always the glossae which are reduced while the paraglossae are well developed.
Moreover, Professor Kellog offers no explanation of the median
thickening, the position of which is typical of the glossae.

PROPHARYNX AND HYPOPHARYNX: - The propharynx and hypopharynx are also generalized.

Frontal-Lobe--Epipharynx (Pl. X):- In the propharynx,



which is an extension of the dorsal wall of the pharynx, there has been no differentiation into frontal-lobe and epipharynx. The combined frontal-lobe and epipharynx lines the entire labrum, and is of the exact shape of this sclerite. The distal end is roundly pointed and covered with fine setae which point toward the opening of the pharynx.

Behind the distal setaceous area there is a semi-circular-shaped band which is darker in color, and in the clear space between this band and the setaceous tip there are several sensory pits. Extending from the distal end of the darker band about two-thirds of the length of the frontal lobe there is a clear line on the meson, on each side of which are smaller sense organs. On each side of this middle line there is a hyaline band which extends to the proximal end of the frontallobe-epipharynx and which is produced there into two horn-like processes which extend proximo-laterad. These bear a few large sensory pits. On the lateral margin of each of these there is a shallow emargination in which the distal end of the fulcrum articulates. The lateral margins of the frontal-lobeepipharynx are pitted with many tiny sensory pits. These are largest on the lateral margins, decreasing in size towards the meson.

Fulcrum (P1. X):- The fulcrum consists of two curving, hyaline bars extending from the pharyngeal opening along the lateral margins of the propharynx to the horn-like processes of the frontal-lobe-epipharynx. Each distal end is bluntly



rounded and fits into the shallow acetabulum of one of these processes.

Hypopharynx (P1. X):- The hypopharynx, the extension of the ventral wall of the pharynx, extends from the pharyngeal opening to the distal margin of the ligula, forming the lining of this part of the labium at least. It seems probable that the entire lining of the labium is pharyngeal in origin. The reasons for this interpretation are as follows:-

The labium is formed by the union of the two appendages of the last head, or cervical, segment. Whether one believes that there are six or seven primary head segments, there is no doubt but that the labium represents the fused appendages of the last segment. The sclerites of this segment are represented by the cervical sclerites which are often entirely wanting. If present, they are either closely associated with the head capsule or are present as tiny free sclerites in the neck membrane which are often articulated with the head and with the thorax. When they are entirely wanting, this segment is represented only by the neck membrane connecting the head capsule and the thorax, and to which the labium is attached, either at the margin of the occipital foramen or at the end of a gula, which is morphologically part of this membrane.

In the embryo the appendages of this segment are developed caudad of the other head appendages, and widely separated.

During embryonic development they migrate cephalad and mesad, fusing on the meson, to form the labium. On their dorsal sur-



face they form the floor of the mouth cavity. The labium is thus originally a hollow appendage with two sides, one on the ental and one on the ectal surface. It is the ental surface which forms the true lining of the labium. This is a different condition from that found in the labrum which is a sclerite of the head. It is a single flat piece which has no lining of itself.

During the embryonic development, however, the wall of the pharynx splits on it's lateral margins near the mouthopening. The dorsal wall of the propharynx proceeds cephalad and forms the lining of the ental surface of the clypeus and labrum. The ventral wall, or hypopharynx, proceeds forward to the proximal end of the labium where it joins the ental surface, or lining, of the labium at it's proximal end. This is the most generalized condition possible, and it is the exact condition found in a Carabid larva, in which form the labium is hollow and the hypopharynx extends only to the proximal margin of the submentum. This primitive condition, however, is not a general one. The tendency is for the labium to flatten out, for the ental surface to adhere to the ectal surface, forming a single flat piece like the labrum of an adult insect, and for the hypopharynx to develop and grow disto-dorsad of the ental surface of the labium and form the real lining of the labium and the floor of the buccal cavity. This is undoubtedly the condition found in a more highly specialized chrysomelid larva and in a sphinx larva. In both these forms



the labium is completely flattened and forms a single thin membrane with the hypopharynx extending to the distal end of the labium, where the two parts fuse. There is a hollow between the two parts, but the lining of the labium and floor of the mouth cavity is pharyngeal, not labial, in origin; the salivary ducts which open into the buccal cavity at the distal end of the labium being considered evidence of this, as these ducts always open through the lingua, the median part of the hypopharynx.

In Corydalis the salivary duct opens entad of the proximal margin of the ligula, and the part of the hypopharynx proximad of this point and the part distad of it are separated by a slight furrow, but there is not a distinct suture. There is a perfect suture, however, around the entire margin of the ligula, between it and the lining, exactly as there is a distinct suture between the labrum and the propharynx. If this lining were part of the labium instead of part of the hypopharynx, there would not be a distinct suture around the margin and there probably would be one between this lining and the distal margin of the hypopharynx entad of the proximal margin of the ligula. This is the condition in the carabid larva. Where the labium is not lined with an extension of the pharynx, there is no suture between the two surfaces of the labium.

Taking all these points into consideration, it seems probable that originally the floor of the buccal cavity was



lined by the ental surface of a hollow labium formed by the two appendages of the seventh segment, but as the forms become more specialized the tendency is for the two surfaces of the labium to meet, adhere, and fuse, and for the hypopharynx to grow out over the ental surface and form the true lining of the buccal cavity.

The hypopharynx from the pharyngeal opening to the proximal margin of the ligula is a thin membrane covered with tiny triangular proximal-pointing papillae. The opening of the salivary duct is on the meson of the hypopharynx just proximad of the lining of the ligula.

Superlinguae (P1. X):- The superlinguae which are originally paired have become fused in this insect on the meson and form a heavily chitinized band across the hypopharynx at the pharyngeal opening. This band is broad at the middle but narrowed on the lateral margins. The ends extend onto the dorsal wall or propharynx, and articulate against the proximal ends of the fulcrum.



III. A CARABID LARVA

As in Corydalis, the mouth opening of this coleopterous larva is directed cephalad, but the head is longer, narrower, and much thinner than is that of the new opterous larva. It is also very strongly chitinized, making dissection much more difficult. The larva shows also about the same degree of specialisation as the larva of Corydalis; the same sclerites are distinct and the same sutures present, with one notable exception in the case of the gula which is present in a well developed form in Corydalis and is apparently absent in the carabid larva.

FIXED PARTS OF THE HEAD

The fixed parts of the head, consisting of the head capsule and the tentoium, are all very heavily chitinized andextremely brittle in this insect.

Epicranial Suture: (Pl.XI):- The epicranial suture extends from the caudal to the cephalic margin of the head. For a short distance it extends as a wide gap on the meson, which is filled in by a delicate membrane. About one-third of the length of the head capsule from the caudal margin it branches, each arm proceeding latero-cephalad until it reaches a point mesad of the caudal margin of the ocularium. At this point each arm turns and proceeds directly cephalad to the margin of the head capsule.

Vertex (Pl. XI):- The vertex is the region on the dorsal aspect of the head on each side laterad of the epicranial suture. It extends from the caudal margin to the cephalic mar-



gin of the head. The cephalic margin of the vertex on each side of the arms of the epicranial suture is on a level with the distal end of the suture and is not declivious. Near the latero-distal angle on each side of the dorsal aspect there is on the vertex the ocularium, the region bearing the simple eyes. This is not really visible from a dorsal aspect, but is entirely visible from a lateral aspect. The simple eyes are arranged in the form of a rosette. On the middle of the dorsal margin of the ocularium between two of the simple eyes there is a large setigerous puncture, the supra-orbital setigerous puncture.

The vertex extends on to the ventral aspect of the head where it is fused with the genae for it's entire length on each side. At the cephalic margin of the head, on the ventral aspect, near the lateral margin of the head just mesad of the antennal socket the vertex is separated by a distinct suture from the sclerite mesad of it, the postgena.

The antennal socket of each side is located at the extreme lateral and cephalic margins of the head and is apparent on both the dorsal and ventra aspects of the head, cephalad of the ocularium. At the caudal margin of the vertex and surrounding the occipital foramen, there is an extremely narrow band. This is an extension of the posterior arms of the tentorium. The condition of the vertex is the same as in the larva of Corydalis except that in Corydalis the occiput is on the dorsal aspect and separates the vertex from the occipital for-



amen, while in this species the occipital suture does not extend on to the dorsal aspect so that the vertex extends caudad to the occipital foramen, on the dorsal aspect.

Front-Clypeus(Pl. XI):- The region mesad of the two halves of the vertex and between the arms of the apicranial suture is the front. The caudal one-third is triangular in outline, the apex of the triangle being directed caudad. The cephalic two-thirds is rectangular in outline, this part being nearly three times as wide as long. It is completely fused on its cephalic margin with the sclerite distal of it, the clypeus, which is not divided into a first and second clypeus by a transverse suture in this species. However, the invaginations of the anterior arms of the tentorium mark the proximal angles of the clypeus, so that the line of fusion of the front and clypeus may be determined accurately, as the fronto-clypeal suture, when present, extends transversely between the two points of invagination of the anterior arms of the tentorium.

The area which extends beyond the cephalic margin of the head capsule is composed of four sclerites, the longest of which is the clypeus. This is fused on the proximal margin with the front, but is separated from the sclerites laterad and distad of it by distinct sutures. The clypeus is roughly rectangular in shape, being of the same size as the cephalic two-thirds of the front. It is slightly narrower at its distal than at its proximal margin. The shape differs from that of Corydalis, which is narrower and longer, and there is absolutely no trace



in the carabid of a suture dividing it into a first and second clypeus.

Antecoxal Pieces of the Mandibles (Pl. XI):- The antecoxal pieces of the mandibles are the small sclerites located laterad of the clypeus. The suture separating each one from the clypeus extends from the proximal angle of the clypeus meso-distad to very near the distal margin of the clypeus and then curves back, laterad, to the margin of the projecting area. The antecoxal pieces are small, narrow, and triangular in outline. As in Corydalis, these are completely fused with the clypeus in the adul form.

Labrum (P1. XI):- The labrum is located cephalad of the clypeus. It is of the same width as the clypeus and so narrow that unless specimens are cleared and mounted, the labrum will not be seen at all. This is very different, also, from the larva of Corydalis which has a long, narrow, movable, flap-like labrum. In Corydalis the second clypeus and labrum together make a long flap which extends cephalad almost to the end of the mandibles, which are articulated against the antecoxal pieces along their cephalic border. In the carabid larva they are articulated in the proximal angles of the antecoxal pieces and the entire clypeus and labrum extend only a short distance cephalad of their points of articulation. Along the distal margin of the labrum there is a fringe of ten long, narrow setae on each side.

Occiput (Pl. XII): - On the ventral aspect of the head



next to the occipital foramen there is on each side a sinuately diamond-shaped sclerite. These two sclerites form the occiput. At their mesal angles they are closely approximated, but diverge caudad of this point. The occipital suture is divided into two parts, each part extending laterad from the caudal end of a long.narrow membrane, which is on the meson of the ventral aspect of the head. Each of these sclerites is sinuate and extends to the lateral margin of the ventral aspect, where it reaches the margin of the occipital foramen so that the occiput is confined entirely to the ventral aspect of the head, while in Corydalis the occiput was confined entirely to the dorsal aspect. The occiput is homologized by Comstock as the "united tergal portions of the postgenae". In Corydalis the suture separating these portions of the mandibular segment extends to the epicranial suture on the dorsal aspect, so that the two tergal parts are closely approximated, but not united on the meson of the dorsum. The suture, however, meets the occipital foramen on the lateral aspect so that it is confined entirely to the dorsum. In an adult carabid, Harpalus caliginosus, the occiput is present both on the dorsal and ventral aspects, the occipital suture running across the entire dorsal aspect onto the ventral where it becomes obsolete on each side near the gular sutures, the two terga being united on the meson of the dorsum without any indication of a suture. In the larva of this carabid these portions of the postgenae do not extend onto the dorsal aspect, but are cut off by the meeting of the



occipital sutures and the occipital foramen. The two pieces of the occiput are margined by a continuation of the narrow bands which separate the vertex from the occipital foramen, and which are a part of the posterior arms of the tentorium.

It is probable that the difference in the position of the occiput in the two forms is due to the difference in the feeding habits of the two forms. In Corydalis the head, although the mouth-opening is directed cephalad, is tipped slightly ventrad so that the support is needed on the dorsal side. In the carabid larva, the head is tipped dorsad, the prey is punctured by the mandibles and held up so that the juices may run down into the buccal cavity. In order to maintain this position, a strong support is required on the ventral aspect of the head. This is furnished in part by the two pieces of the occiput.

Gula (P1. XII):- In Corydalis, both the larva and the adult, there is a large and well developed gula. In adult carabids, also, the gula is prominent. This condition is not found, however, in this carabid larva. The genae are separated only by a narrow median membrane which extends the entire length of the head on the meson and is the homologue of the gular sclerite in Corydalis or in adult carabids. As the gula is an indication of specialization, it may be concluded that in this respect this beetle larva is more generalized than the larva of the neuropteron. The gula is developed when the head is rotated so that the mouth opening is directed cephalad.



In the forms where the mouth-opening is directed ventrad, the mouth-parts are attached to the cervical membrane at the margin of the occipital foramen. Where the mouth-opening is directed cephalad there needs to be some part to fill in the gap between the occipital foramen and the mouth-parts. This is accomplished by the pulling forward of the membrane of the neck, to which the labium is attached. This membrane is subsequently chitinized and incorporated in the head capsule in the shape of a gula which is characteristic of all generalized Coleoptera. In Corydalis the typical condition of a gula is found. but in this carabid we have probably an early stage in the development of a gula, the neck membrane extending down the meson to the cephalic margin of the head where the labium is attached, and only indicating the possibility of the development of a prominent gula from this tiny membrane. ference in the size and the extent of the gula in the two forms is great, but the homology is the same in both cases.

The gula is undoubtedly developed from a part of the neck. As the neck or microthorax is really homologous with the last cephalic somite, which has as its appendages the labium, the gula is formed by the sternal element of the last head segment.

Genae (Pl. XII):- Each gena is located on the ventral aspect of the head, cephalad of the occipital suture and laterad of the gular membrane. Each one extends laterad to the lateral aspect of the head where it is fused for its entire length with the vertex without any indication of a suture. In Cory-



dalis the genae are widely separated by the stem of the T of the gula; in this beetle larva they are closely approximated, being separated only by the narrow gular membrane. The cephalo-mesal portion of each gena is separated from the cephalic margin of the head capsule by a lateral expansion of the gular membrane. The cephalo-lateral portion is separated from the cephalic margin by the postgena.

There is a furrow on each side extending from a point mid-way between the caudal and cephalic margins of the head, just laterad of the gular membrane, disto-laterad to the cephalic margin of the head. This appears at a glance to be a suture, but is in reality a furrow caused by the close attachment of one of the branches of the posterior arm of the tentorium to the ental surface of the head capsule.

Postgenae (Pl. XII):- The narrow sclerites cephalad of the genae and mesad of the antennal sockets are the postgenae. Each postgena is one-third as broad as the entire head and is only one-fourth as long as broad. In the middle of the distal margin there is a round acetabulum into which a condyle of the mandible fits. At the meso-cephalic angle of the postgena there is a slight projection which is increased in size by the knob-like enlargement of one of the branches of the posterior arm of the tentorium which terminates at this point. It is against this khob-like projection of each side that the cardo of each maxilla articulates.

TENTORIUM: - The condition of the tentorium is very gen-



eralized, as might be expected from the high degree of generalization shown in the exoskeleton of the head. It is very similar to the tentorium of Corydalis, except that there is a greater development of the posterior arms.

Anterior Arms (Pl. XIII):- The points of invagination of the anterior arms of the tentorium may be seen as slits extending for a short distance caudo-mesad from the proximal angles of the clypeus. From these invaginations the arms proceed caudo-mesad through the head cavity, and fuse with the posterior arms, near their points of invagination. They thus form a pair of oblique pillars in the head cavity. Cephalad of the point of invagination each anterior arm projects into the angle between the clypeus and the front, forming a buttress-like projection, against which the mandible articulates.

Dorsal Arms: (Pl. XIII): - The dorsal arms are invaginated on the lateral aspect of the head on each side between the ocularium and the antennal socket. They extend meso-ventrad and caudad as free pillars in the head cavity and fuse with the anterior arms about half-way between the invagination of the anterior and posterior arms. This is different from the larva of Corydalis, where the dorsal arms were closely applied to the head capsule and fused with the anterior arms at the points of their invagination.

Posterior Arms (Pl. XIII):- The posterior arms are invaginated in two prominent pits located on either side of the gular membrane about half-way between the caudal and ceph-



alic margins of the head. There is a branch of each posterior arm which extends disto-cephalad from the point of invagination to the cephalo-mesal angle of the post-gena. These diverging branches are closely applied to the ental surface of the head, and give the ventral aspect the appearance of having two oblique sutures extending from the points of invagination of the posterior arms of the tentorium to the cephalic margin of the head, and which apparently mark the lateral boundaries of the gula.

At their distal ends each anterior branch is enlarged to form a knob-like projection at the mesal angle of the postgena with which the cardo of the maxilla is loosely articulated. From the points of invagination of the posterior arms of the tentorium there is, on each side, a branch which extends caudad along the lateral margin of the gular membrane to the caudal margin of the head. From this point each arm diverges and surrounds one-half of the occipital foramen. The two branches extend on the dorsum to the lateral margin of the narrow membrane which marks the stem of the epicranial suture. It is these branches which form the narrow bands that margin the vertex and occiput. The posterior arms in Corydalis show only a slight caudal and cephalic projection. In this coleopterous larva these projections constitute a large part of the tentor-There is no fusion of the anterior or posterior arms to ium. form a frontal plate or a body of the tentorium.

MOVABLE PARTS OF THE HEAD

The movable parts of the head show a generalized condi-



tion and are similar to the movable parts of the head of Corydalis.

MANDIBLES (Pl. XIII): - The mandibles are long and slender, projecting some distance beyond the margin of the head. are curved in the shape of a sickle, and pointed. At the middle of the mesal margin of each there is a single short projecting tooth mesad. The proximal end is expanded bulb-like, and on both the dorsal and ventral sides there is a strong prominent condyle. That on the dorsal side is nearer the meson than that on the ventral side, is shorter and broader, and has a shallow acetabulum at the end. Into this acetabulum the buttress-like extension of the anterior arm of the tentorium articulates under the proximal angle of the antecoxal piece of the mandible. This articulation is not visible from a dorsal aspect of the head. The condyle on the ventral side is long and slender. It is constricted at the base and expanded at the end into a distinct knob. This condyle fits into a deep acetabulum on the distal margin of the postgena. The lateral margin of the mandible between the two condyles is strongly convex, fitting under the antennal socket against the margin of the head capsule. The large mandibular tendon is attached mesad of the dorsal condyle.

MAXILLAE (P1. XIV):- The general shape of the maxillae is very like that of the maxillae of Corydalis. They are long and rectangular, projecting a long distance beyond the margin of the head capsule and bearing at their distal ends two seg-



mented appendages. Unlike Corydalis, the tips of the maxillae are not retracted within the distal end of the stipes.

Cardo (P1. XIV):- The maxilla is articulated with the postgena at the meso-distal angle of this sclerite. There is a little knob-like projection formed by the angle of the postgena and the enlargement of the cephalic branch of the posterior arm of the tentorium, in which there is a small acetabulum. Into this the maxilla articulates. The cardo is composed of two entirely distinct and widely separated sclerites which are only attached by the buccal membrane. One of these lies on the ventral aspect, but curves around onto the dorsal aspect of the maxilla in a blunt point. In mounted preparations the ental surface of this sclerite is seen from a dorsal view. It extends only two-thirds across the entire width of the maxilla from the lateral margin. In the center of the proximal margin there is a rounded protruding condyle which articulates with the postgena.

The second sclerite of the cardo lies also on the ventral side. This sclerite is triangular in outline, the apex of the triangle being directed laterad. The mesal margin of this triangle is continued onto the dorsal side in a short projection, and rests against the superlingua.

The articulation between the cardo and the distal part of the maxilla is entirely between the first sclerite of the cardo. The lateral two-thirds of the distal margin of this sclerite rests against the proximal margin of the distal por-



tion. The mesal angle of the distal portion of the maxilla, which is extended into a small prominence, rests in the hollow of the mesal curve of the second sclerite of the cardo.

Stipes(Pl. XIV):- The distal part of the maxilla is three times as long as broad, and is slightly wider at its proximal than at its distal end. It is narrowest at the middle where it is bent mesad at a very slight angle. The largest sclerite of this distal portion is the stipes, which extends distad from the cardo to the margin of the maxilla. On the ventral aspect it comprises nearly the entire maxilla, on the dorsal aspect it occupies only about one-half of the total area of the maxilla, the mesal half being occupied by a setaceous sclerite. The stipes is entirely bare, and generally membranous. On the dorsal aspect, the proximal margin is more heavily chitinized.

Palpifer (P1. XIV):- The palpifer occupies about the same area on both the dorsal and ventral aspects of the maxilla. On each side it is triangular in outline, the apex of the triangle being on the lateral margin of the maxilla, one-third of the distance between the proximal and distal margins of the stipes. The base of the triangle is one-third the width of the maxilla. The palpifer is more heavily chitinized than the rest of the maxilla, and bears a single very long seta on the middle of the lateral margin. It does not extend to the palpus on the ventral aspect.

Maxillary Palpus (Pl. XIV):- The maxillary palpus is a



four-segmented appendage, borne at the distal margin of the palpifer on the dorsal side. The proximal segment is one-half the width of the maxilla and is as broad as it is long. The second segment is twice as long and slightly narrower, the third is subequal in length to the second, but narrower. The distal segment is very short and narrow and roundly pointed at the tip. The entire palpus is glabrous with a few scattered sensory pits.

Subgalea (P1. XIV):- The subgalea is the sclerite occupying the mesal half of the dorsal aspect of the maxilla. It extends from the cardo to the distal margin of the maxilla. The suture separating it from the stipes is irregular and very fine. The subgalea is slightly narrower at the middle than at either end. The entire sclerite is covered with irregularly arranged, long setae.

Galea (P1. XIV):- The subgalea bears at its distal end a short two-segmented appendage, mesad of the maxillary palpus. This is the galea. The segments are subequal in length, the second being much narrower than the first.

Lacinia (Pl. XIV):- Along the mesal margin extending the entire length of the maxilla, there is a long, narrow, densely setaceous sclerite, the lacinia, mesad of the subgalea. At it's distal end it is prolonged into a short, triangular projection. The form and position of the lacinia are the same as they are in the larva of Corydalis. In an adult carabid, Harpalus caliginosus, the position of the lacinia has been shifted



just as it has in the adult of Corydalis. That is, the stipes is shortened, and the lacinia shifted distad, with the small projection of the larval maxilla developed into a large, free, setaceous appendage, curved and directed laterad.

attached to the end of the gular membrane and extending beyond the distal margin of the labrum, so that its ental surface is plainly visible from a dorsal aspect of the head. It is round, tube-like in shape, in this respect being more generalized than the forms in which the two sides have fused, forming a perfectly flat piece.

Submentum (Pl. XV):- The submentum is a round, ring-like sclerite which is hollow, and which is attached on it's ectal surface to the distal end of the gular membrane. There is no definite suture separating the gular membrane and the submentum. On its dorsal ar ental surface it is attached at the proximal margin to the distal end of the lingua. The ental surface is thin, membranous, and entirely bare with a few scattered papillae. The dorsal surface is covered with long, curly setae which conceal the union with the hypopharynx and which extend cephalad over the distal part of the labium.

Mentum (Pl. XV):- The mentum is confined entirely to the ventral aspect. It is a small, narrow band which does not extend to the lateral aspects, between the submentum and the ligula. It is slightly more heavily chitinized than the submentum, and is produced on the meson into a long, narrow projection extending cephalad on the meson of the ligula.



Ligula (Pl. XV):- The ligula is the largest and most conspicuous part of the labium. It is more heavily chitinized and longer than the submentum, comprising all the labium distad of the submentum on the dorsal side and distad of the mentum and submentum on the ventral side.

Palpigers (P1. XV):- The palpigers are broad, shoulderlike sclerites on the lateral margins of the labium, extending
from the distal end of the submentum to the end of the ligula.

Each occupies one-third of the ligula on both the dorsal and
ventral sides. The palpigers are covered with sharply pointed,
broad, strong setae, which are more numerous on the dorsal
and lateral surfaces. At the meso-distal angle on the ventral
side of each palpiger there is a long seta which projects distad of the middle of the first segment of the palpus, and near
the meso-proximal angle there is a single short and very sharply pointed seta.

Labial Palpi (Pl. XV):- The labial palpi are borne at the distal ends of the palpigers at each lateral margin of the labium. Each is a two-segmented appendage a little longer than the ligula. The segments are subequal in length, the second being narrower than the first and slightly narrowed to a truncate point, on which there are extremely minute organs of special sense. The palpi are entirely smooth.

Glossae (Pl. XV):- The glossae and paraglossae are not well defined. The glossae are fused to form a median knob at the distal end of the ligula, which is slightly more chitin-



ized than the regions laterad of it, and which bears two extremely long setae projecting beyond the first segment of the palpus. This little knob is the homologue of the glossae, which are present in the form of well-defined lobes in the adults of the more generalized ametabolous forms. It is in about the same condition as the glossae in the larva of Corydalis, and is similar in appearance to the same structure in the adult carabid, Harpalus caliginosus.

Paraglossae (Pl. XV):- the paraglossae constitute all the region of the ligula, mesad of the palpigers, excluding the tiny glossae. They extend on the ventral side from the mentum, on the dorsal side from the submentum to the distal margin of the ligula. The dorsal surface is covered with long, curly setae, similar to thos on the submentum, while the ventral side is smooth.

PROPHARYNX AND HYPOPHARYNX (Pl. XVI):- This carabid larva shows a much more generalized condition of the propharynx and hypopharynx than is present in the larva of Corydalis or even in the adults of the more generalized ametabolous forms, such as the cockroach or the grasshopper. There is very slight development of the walls of the pharynx. The buccal cavity is very short, the propharynx and hypopharynx extending only a short distance cephalad of their point of union. This is in striking contrast to the condition found in the larva of Corydalis or the adult of Periplaneta where the dorsal and ventral walls extend some distance cephalad of their point of union,



which is entad of the fronto-clypeal suture, and form a large buccal cavity.

very much widened and completely lining the labrum and part of the clypeus, is simply a loose lining entad of the clypeus. It is attached to the sides of the clypeus by a homogenous, cuticular membrane which is derieved from the propharynx. This broad, narrow band of the propharynx shows absolutely no indication of differentiation into frontal lobe, fulcrum and epipharynx. They are all combined in a narrow band which is densely covered with extremely fine, long setae, arranged regularly in rows and packed closely together, which give the propharynx the appearance of being striated. Caudad of the opening into the pharynx, the dorsal wall of the pharynx has several rows of bluntly rounded papillae.

Hypopharynx (Pl. XVI):- The ventral wall of the pharynx extends a little farther cephalad than the propharynx, but only to the cephalic margin of the head capsule and not cephalad over the ental surface of the labium, as it does in the larva of Corydalis. It is of the same width as the submentum. The hypopharynx may be differentiated into the lingua and the superlinguae.

Lingua (Pl. XVI):- The lingua is the median, unpaired portion extending nearly the whole width of the hypopharynx. It is hyaline in color and densely, irregularly setaceous. It is on the lingua that the salivary ducts open in all the



more generalized forms and in Lepidoptera, the silk ducts, which are homologous with the functional salivary glands of more generalized orders. In this larva there is not a trace of any duct opening through the hypopharynx, and there were no salivary glands or ducts discernible upon dissection. It is in probable that they are entirely lacking, this form. Henneguy says that salivary glands are not constant and that many of the Pentamera lack them.

Superlinguae (Pl. XVI):- Along the lateral margin of the hypopharynx extending latero-distad from the pharyngeal opening, there is on each side a more heavily chitinized, rod-like projection with a double-pronged end, each prong being bluntly rounded. These projections are the superlinguae, each one articulating with the mesal margin of the second sclerite of the cardo.

Pharyngeal Sclerites (Pl. XVI):- Caudad of the pharyngeal opening the walls of the pharynx are supported by a pair of long, slender, sinuate sclerites, located along the lateral margins of the pharynx. These are the pharyngeal sclerites.



IV. XYLORYCTES SATYRUS

This large scarabaeid is quite different from the coleopterous larva previously studied. The head has been secondarily rotated caudad so that the mouth opening is directed ventrad, and the mouth-parts have consequently been pulled back toward the margin of the occipital foramen and the gula, which is such a large and well developed sclerite in the adult carabid, Harpalus caliginosus, and which is represented by the long gular membrane in the carabid larva, is much reduced. The mouth-parts have been modified to form an efficient grinding apparatus. The mandibles and hypopharynx interlock in such a way as to form a mill at the entrance to the buccal cavity.

FIXED PARTS OF THE HEAD

The condition of the fixed parts of the head is very different from the condition found in either of the previously studied forms. This difference is due in great part to the ventral position of the mouth opening and to the shape of the head, which is large and round, in contrast to the shape of the head of the carabid, which is long and flat.

Epicranial Suture (Pl. XVII):- The epicranial suture extends in a straight line down the meson from the margin of the occipital foramen for one-fourth of the entire length of the head, where it divides, the two branches extending ventrodistad for another fourth of the length of the head at an acute angle. From these points the two arms extend down the ventral



half of the head capsule in a broad curve to the mesal margins of the antennal sockets.

Vertex (P1. XVII):- The vertex is the region on the cephalic and dorsal aspects of the head laterad of the epicranial suture. It is fused on the caudal aspect with the genae without and indication of sutures. The antennae are borne in sockets at the lateral angles of the cephalic aspect, but are visible from all aspects. The ocularium is situated on each side on the vertex dorsad of the antennal socket on the lateral aspect of the head. The eyes are very poorly developed, there being but two inconspicuous, simple eyes. This condition is closely correlated with the habits of this beetle larva, which lives among dead leaves and decaying vegetable matter, about two inches below the surface of the ground. There are several long setae on the ocularium, and on the cephalic aspect between the eyes and the epicranial suture there is a single, large, setigerous puncture.

Front (Pl. XVII):- The front is the large triangular sclerite mesad of the arms of the epicranial suture, which is nearly as wide at the ventral margin as the head capsule. It extends ventrad only as far as the margin of the vertex. One quarter of its width mesad from the antennal sockets it is projected on each side into a small, triangular protuberance which fits over the proximal angle of the clypeus.

Clypeus.(Pl. XVII): - The clypeus is a broad, short piece at the ventral margin of the front. Unlike the forms previously studied, it is separated from the front by the fronto-



clypeal suture which extends between the proximal angles of the clypeus. The clypeus is not divided into a first and second clypeus by a transverse suture, and the antecoxal pieces of the mandibles, which are present in the larvae of Corydalis and the carabid beetle, are completely fused in this insect with the clypeus. The clypeus is a little more than one-half as wide as the front, and is twice as wide as long. Near the ventral margin on either side there are two setae. One of these is very near the lateral margin, the other is located, one-sixth of the width of the clypeus, mesad of it.

Labrum (Pl. XVII):- The labrum is the flap borne at the ventral margin of the clypeus. There is a sharp, triangular emargination at the proximal angle between the labrum and the clypeus. Each lateral margin is rounded in a broad curve from these angles to a slight emargination at the middle of the ventral margin of the labrum. The entire margin is fringed with tiny setae. At each proximal angle there is a pair of setae, and another pair of the same length directly ventrad of them adjacent to the curved lateral margin. On each side of the meson, two-thirds of the distance between the dorsal and ventral margins, there is a single seta. Laterad of these on the ventral margin is another pair which is much shorter than the other labral setae.

Trochantin of the Mandible (Pl. XVII):- Although the antecoxal pieces of the mandible are entirely fused with the clypeus, the trochantin of the mandible, which Comstock be-



lieves to be homologous with the trochantin of a thoracic leg, is present. There is a crescent-shaped sclerite on each side of the head between the cephalic and caudal articulations of the mandible separating the mandible from the head capsule, ventrad of the antennal socket. On the cephalic aspect it does not extend mesad to the angle of the clypeus and front, but the suture forming it's ventral margin curves up to the ventral margin of the front, laterad of the clypeus. In the angle between the trochantin of the mandible, the clypeus, and the front the mandible articulates. On the caudal aspect of the head the trochantin of the mandible extends mesad to the lateral margin of the projection of the ventral margin of the head capsule, with which the ventral condyle of the mandible articulates.

Genae (P1. XVII):- Owing to the secondary rotation of the head and the resultant shortening of the gula, and to the drawing back of the mouth-parts toward the occipital foramen, there is very little of the head capsule present on the caudal aspect of the head. Moreover, the membrane of the neck is folded back from the occipital foramen over the head capsule so as to conceal most of the caudal aspect in a natural position.

The genae are the large sclerites which fuse with the vertex near the lateral margin of the caudal aspect of the head. Each is separated from the sclerite mesad of it, the postgena, by a suture extending dorsad from a point on the



ventral margin of the head capsule, one-third of the distance between the occipital foramen and the lateral margin of the head. This suture becomes obsolete before it reaches the occipital foramen, so that for a short distance each gena is fused with the postgena. At the mesal angle of the ventral margin of the gena there is a short, blunt projection in which there is an acetabulum. It is in this acetabulum that the ventral condyle of the mandible articulates.

Postgenae (P1. XVII): - Each postgena is situated between the gena and the occipital foramen. The two postgenae do not meet on the meson ventrad of the occipital foramen, but are widely separated, the occipital foramen being bridged by the body of the tentorium. The postgenae are long and narrow. They are attached along the margin of the occipital foramen to the cervical membrane. At their mesal angles the posterior arms of the tentorium are invaginated. These invaginations are seen as long slits between the postgenae and the overlapping cervical membrane. It may be mentioned at this point that the maxillae, which normally articulate against the postgenae, do not do so in this insect. This fact will be discussed later.

Gula (P1.XVII):- As the head of the scarabaeid has been secondarily rotated, the gula has necessarily been reduced in length. The mouth-parts have been drawn back and the head shortened so that the gula is attached to the cervical membrane at the margin of the occipital foramen and extends ven-



trad of the other parts of the head capsule, which are laterad and dorsad of the foramen, and forms the proximal half of the lower lip. It is not chitinized, but is composed of a hyaline membrane which is rhomboidal in out-line, the dorsal margin, which is attached to the gular membrane, being widest. The proximal angles are produced laterally to form more heavily chitinized condyles which fit into the acetabula of the cardines of the maxillae. This articulation replaces the more usual one with the postgenae.

The gula is attached along each lateral margin to the stipes, forming a broad closed floor on the caudal aspect of the head. If it were not that these parts were joined by the buccal membrane, the membrane which in the more generalized types only connects the proximal ends of the mouth-parts and which is expanded in this insect, there would be no floor on the caudal aspect, and the mouth opening would be directly into the occipital foramen. The labium and maxillae distad of the gula are entirely free.

TENTORIUM: (Pl. XVIII): - The tentorium of Xyloryctes shows great differences from the tentorium of either of the forms previously studied. These differences are due in part to the greater development and more intricate relationship of the different parts, and partly to the differences in the shape of the heads. In this insect the parts of the tentorium are all closely applied to the head capsule. The greatest difference is in the dorsal arms which in the carabid larva and Corydal is ex-



tended onto the dorsal aspect of the head and are fused with the anterior arms. In this insect each dorsal arm extends on to the caudal aspect of the head and is associated entirely with the posterior arms.

Anterior Arms (Pl. XVIII): - The anterior arms are invaginated at the proximal angles of the clypeus; the points of invagination do not show at all externally. From these points the anterior arms extend directly mesad along the frontoclypeal suture, fusing on the meson and forming the frontalplate of the tentorium. This is a greater development than in the other forms, in which there was no frontal-plate. this form there are no pillars extending from the points of invagination of the anterior arms, through the head cavity to the posterior arms. Consequently, there is no connection between the anterior arms and other parts of the tentorium. At the lateral ends the anterior arms are expanded into buttresslike projections which are just entad of the angle between the front and the clypeus. There is an acetabulum on the cephalic side of the mandible into which the expansion of the anterior arm fits, forming the cephalic articulation of the mandible.

Posterior Arms (Pl. XVIII):- The posterior arms are invaginated between the mesal angles of the postgenae and the cervical membrane. The invaginations may be easily seen as long slits, but they are ordinarily concealed by the folding back of the cervical membrane over the caudal aspect of the head. From the invaginations on each side a broad band extends mesad. The two branches fuse on the meson forming a



broad. heavy bridge across the occipital foramen entad of the cervical membrane. This is the body of the tentorium. ventral half of this bridge is considerably more chitinized than the dorsal half. On each side of the ventral margin of the body of the tentorium there is a short, bluntly pointed projection. The large mandibular tendon is attached to this. The ventral half of the body of the tentorium is continued laterad along the ventral margin of the postgena to the suture between the postgena and the gena. The branch at this point turns at a right angle and divides. One branch proceeds dorsomesad across the postgena almost to the dorsal end of the slit marking the invagination of the posterior arm. This forms an acute angle with the other branch which follows the suture between the gena and postgena for its entire length, and which is fused on its dorsal one-third with a branch of the dorsal arm.

The dorsal and less heavily chitinized half of the body of the tentorium extends dorsad around the margin of the occipital foramen. It appears as a white, thick, leathery membrane surrounding the occipital foramen. It is attached all the way to the cervical membrane, which on the caudal aspect folds back from the band of the tentorium over the postgenae. This band is also attached to the postgenae and vertex, which border on the occipital foramen. These branches meet and fuse on the meson of the dorsal aspect at the base of the epicranial suture. From the point of fusion there is a slender med-



ian projection which extends, closely applied to the head capsule, along the stem of the epicranial suture, ventrad to the point of division of this suture. On the caudal aspect of the head dorsad of the point where the suture between the gena and postgena becomes obsolete, there is a short lateral projection on each side from the band of the posterior arm which surrounds the occipital foramen, which extends as a curved irregular projection over the ental surface of the cervical membrane.

Dorsal Arms (Pl. XVIII):- The dorsal arms are attached to the ental surface of the vertex on each side between the ocularium and the antennal socket on the lateral aspect of the head. The points of attachment do not show externally. From the point of attachment each dorsal arm extends mesad along the suture between the gena and the trochantin of the mandible. Near the mesal angle of the gena the dorsal arm forms the heavily chitinized projection with a deep acetabulum in which the mandible articulates. From this projection it extends to the postgenal suture where it turns dorsad, forming a broadly obtuse angle. This branch extends dorsad as a slender, pointed rod the entire length of the suture, closely adjacent to and fused with, for it's dorsal third, the branch of the posterior arm.

MOVABLE PARTS OF THE HEAD

The mouth-parts are very different from the two forms previously studied, the mandibles are much more prominent, the maxillae are not free for their entire length, and the pro-



pharynx and hypopharynx are well developed.

MANDIBLES (P1. XIX):- The mandibles of Xyloryctes are powerful, heavily chitinized, and well fitted for grinding and crushing. They are decidedly asymmetrical, the asymmetrical parts fitting against each other, increasing the efficiency of the molar surfaces. The cephalic or ectal surface is convex, the caudal or ental surface concave and transversely ridged. The bases of the mandibles are rectangular in outline, the molar surfaces being the proximal ends of the mesal margins. The distal end of the mesal margin of each mandible is produced into blunt teeth. The lateral margin is rounded in a broad curve from the proximal to the distal end.

The molars or grinders, as Smith terms them in his paper on Copris carolina, are at the proximal ends of the mesal margins and are the parts which show the highest degree of asymmetry. On the right mandible the molar, which extends half the mesal length, terminates at the proximal end of the mandible in a sharp tooth. The distal end of the molar is bluntly toothed and fits into a concavity on the mesal margin of the left molar. The molar on the right mandible is separated from the rest of the mandible by a longitudinal line-like suture. The question of the homologies of the parts will be considered later.

The molar of the left mandible does not extend to the base of the mandible and is not as long as that of the right.

It is broader at its distal end and forms a prominent projection on the mesal margin which is cut off squarely. The mesal



margin of the distal end is concave, fitting over the molar of the right mandible. From the proximal end of this square projection the molar extends in an uneven toothed line to the main body of the mandible. It may be mentioned here that on the hypopharynx the right side of the superlinguae is produced into a sharp, heavily chitinized tooth which fits against the molars of the mandibles and assists in crushing the food before its entrance into the pharynx and in closing the buccal cavity.

Distad of the molars, the inner margins of both mandibles are deeply emarginate, while the distal thirds of the mesal margins are produced into asymmetrical teeth. The right mandible has a sharp, broad terminal tooth, with a broader, more blunt one proximad of it. The left mandible has a sharper terminal tooth which fits between the two teeth of the right mandible. Proximad of this, the margin is not definitely toothed, but is irregular in out-line and proximad of the proximal tooth; the right mandible is produced into a small, blunt basal tooth. These margins are separated from the rest of the mandibles by line-like sutures. On the caudal surface of each mandible, extending from the ventral condyle to the molar, on the right mandible and to near the mesal margin of the main part of the mandible on the left, there is on the proximal margin a triangular lobe-like sclerite with the base along the base of the mandible. These are entirely separated by a suture from the rest of the mandibles and are not the



chitinized ends of the large mandibular tendons which are attached to the mesal margins of the mandibles.

The articulations of the mandibles are very prominent. On the cephalic side near the lateral margin there is an acetabulum which fits over the projection of the anterior arm of the tentorium in the angle between the front and the clypeus. On the caudal aspect near the lateral margin there is a broad, very heavy condyle which articulates with the postgena. Between these two articulations the proximal margin is concave and fits against the trochantin of the mandible under the antennal socket. The greater part of each mandible extends mesad from the point of articulation entad of the clypeus and labrum, so that the molars are not visible normally, but meet on the meson entad of the clypeus.

J. B. Smith, in his paper on the mouth-parts of Copris carolina, homologizes these parts of the mandible with the different sclerites of a typical appendage. According to his interpretation, the main part of the mandible is homologous with the stipes of the more generalized appendage. The small triangular piece at the base of the caudal surface is the cardo. He interprets the molars as being the subgaleae, and the sclerites which bear the teeth on the mesal surfaces as the galeae. On the mesal margin, extending from the molar to the galea, there is a single slender sclerite which forms on each side the caudal half of the proximal tooth. This arises from the base of the subgalea and is called by Smith the lacinia. In



Copris carolina the galea extends proximad, laterad of this sclerite, to the subgalea also, but in this form this sclerite forms only the terminal part of the mandible. This is evidence against this interpretation, for the galea is always borne by the subgalea.

This interpretation of the homologies appears extremely logical. but it does not seem correct. There is no doubt but that the mandibles have been developed from typical appendages, and that the sclerites which in the maxillae and labium of the more generalized insects are distinct, have fused to form efficient jaws. But if there are forms in which the primary sclerites of a typical appendage are found separated by distinct suture in the mandibles, we should expect them to be among the most generalized insects. In Machilis and Campodea, it is true. there are two parts at the tip which are usually homologized as the galea and lacinia, but even in the most generalized Orthoptera there is not a trace of separate sclerites in the mandibles. In Machilis and Campodea, too, there are not as many of the sclerites present and these are not so distinct as in this specialized coleopterous mandible. In the generalized beetles, the carabids, the mandible is always a single, homogeneous piece. In the more specialized Coleoptera we should not expect to find a reversion to a more generalized condition than is found even in Machilis. Moreover, in the arthropods which are less highly specialized than the insects, the crus-



taceans, specialization has proceeded so far along this line that the parts of a typical appendage are not distinct in the mandibles.

This condition, where the mandibles are divided, is common among the Passalidae and Staphylinidae, and it is probable that it is a secondary modification attendant upon the development of, and the necessity for large grinding surfaces and tearing jaws. These sclerites are undoubtedly due to secondary mechanical causes and are not to be homologized with the primary sclerites of a typical appendage.

MAXILLAE (Pl. XX): - The maxillae are large, well developed organs, laterad of the gula and the labium. They are attached along the lateral margin of the gula by a strong buccal membrance, which is also attached along the proximal margins of the maxillae on the dorsal side, connecting them with the bases of the mandibles, and along the proximal margins of the ventral side, connecting them with the genae and postgenae. The maxillae are much more closely united to other parts of the head than in the forms previously studied. This is owing to the fact that the mouth-parts have been pulled back to near the occipital foramen, and to the fact that the gula is ventrad of the other parts of the head capsule. The buccal membrane is expanded and connects the maxillae and gula so that there is a closed floor on the caudal aspect of the head, and so that the mouth opening is not directly into the occipital foramen. The maxillae are decidedly geniculate. The proxi-



mal part, which consists of the cardo and the greater part of the stipes, extends directly laterad from the gula. At the latero-distal angle of the cardo the maxilla bends and is directed ventrad.

Cardo (Pl. XX): - The cardo, as in the case of the carabid larva, consists of two sclerites which lie on the proximal margin of the proximal part of the maxilla, and which are connected for their entire width with the genae and postgenae by the buccal membrane. The first of these sclerites extends less than half-way from the dorso-lateral angle of the gula to the bend in the maxilla, and is more heavily chitinized along it's ventral margin. It is less than one-fourth as broad as the entire maxilla. The angle of this sclerite, next the gula, is heavily chitinized and hollowed into an acetabulum, which receives the condyle formed by the chitinization of the dorsolateral angle of the gula. This is the main articulation of the maxilla, which serves instead of that more common in biting insects, with the postgena. This change in articulation from the normal type is probably due to the geniculate form of the maxilla. The maxilla has been rotated mesad and its primary direction changed from distad to laterad, with the result that the point of articulation has migrated mesad past the mesal angle of the postgena to the dorsal angle of the gula. The cardo, which normally extends distad from the postgena, extends laterad from the point of articulation.

The second sclerite of the cardo is larger than the first.



It is situated laterad of the first, extending between the first sclerite of the cardo and the angle of the maxilla. It is triangular in out-line on the caudal aspect. The apex is directed meso-dorsad, the base, which is heavily chitinized, latero-ventrad. The second sclerite extends on to the cephalic aspect of the maxilla in a long, narrow fold.

Stipes (Pl. XX):- The stipes comprises a large part of the entire maxilla. On the cephalic surface it comprises all of the maxilla proximad of the angle, and extends beyond the angle, forming part of the ventrad-directed, distal part of the maxilla. On the caudal aspect, it comprises all of the proximal part, ventrad of the cardo. It is, for the most part, a cuticular, non-setaceous membrane. There are two areas of the stipes which have become secondarily chitinized for the support of the maxilla. These areas appear as distinct sclerites. One of them is on the caudal surface of the maxilla, ventrad of the cardo, extending from the gula latero-ventrad nearly to the lateral angle of the second sclerite of the cardo. This appears as a distinct sclerite, but if homologized with the stipes, difficulty is at once encountered, for the palpus and the region bearing the palpus, the palpifer, is not located even near this area. The second area of chitinization is on the ventral margin of the proximal part of the maxilla. This occupies the ventral one-third of both the cephalic and caudal surfaces of the proximal part. It is covered with short, irregularly arranged setae. This could only, if



as the homologue of the subgalea. This is impossible, as the subgalea always bears the lacinia and subgalea, and this setaceous area is not associated at all with the lacinia. The entire area is probably stipes, and these spots have become on the whole chitinized in support of the maxilla, which is, a fleshy, membranous organ. The stipes bears the gula and lacinia, as the suture separating the subgalea has become entirely obsolete, the subgalea being fused with the stipes.

Palpifers (Pl. XX):- On the caudal aspect of the maxilla, the bend in the maxilla is marked by a heavy ridge extending from the latero-distal angle of the cardo ventro-mesad across the maxilla. This ridge separates the palpifer from the cardo and stipes on the lateral half of the maxilla, and the galea from the stipes on the mesal half. The palpifer is on the lateral margin of the distal part of the maxilla, extending half the length from the latero-ventral angle of the cardo to the distal end of the maxilla, and bearing the foursegmented maxillary palpus at it's ventral margin. It is separated from the stipes on its proximal margin by the chitinized, oblique ridge across the maxilla, but is fused for nearly its entire length with the sclerite mesad of it, the galea. There is a short suture extending dorso-mesad from the insertion of the palpuswhich separates the palpifer and the galea for a short distance and which soon becomes obsolete. palpifer extends onto the cephalic aspect in a triangular fold.



This fold is not separated from the stipes by a distinct suture, but the line of union is marked by a slight furrow on which there is a row of twelve large sensory pits. The palpifer is entirely hyaline. The caudal surface is glabrous, but there are a few short setae on the cephalic fold.

Maxillary Palpi(P1. XX):- Each maxillary palpus is a four-segmented appendage attached to the distal margin of the palpifer at the lateral margin of the caudal aspect of the maxilla. The palpus extends only a short distance beyond the distal end of the maxilla. The first segment is short and barrelshaped. The second and third segments are subequal in length, both being longer than the first. On the distal margin of the third there are two long setae with two sensory pits located between them. There are several sensory pits on the second segment. The distal segment, longer and narrower than the third, tapers to a rounded point. This terminal point is less heavily chitinized than the rest of the segment, is entirely covered with small cone-shaped organs of special sense.

Galea (P1. XX):- The galea comprises with the palpifer all the caudal surface of the maxilla distad of the lateral angle of the maxilla. It is fused with the palpifer on its lateral margin. The proximal margin is chitinized, forming a continuation of the ridge between the palpifer and stipes. As this ridge is oblique, the larger part of the galea is distad of the palpifer. The ridge becomes thinner and less heavily chitinized towards the ventro-mesal end, where it turns ven-



trad, forming the mesal margin of the galea. Along the mesal and distal margins of the galea there are two rows of long, strong setae. These are constricted at the base and fit into sockets formed by the outfolding of the cuticle. Along the lateral margin of the galea, distad of the attachment of the maxillary palpus, there is a large, oval clear spot. The galea is bluntly rounded at the distal end and bears a single heavy tooth which is pointed mesad.

On the cephalic side, the galea is of small extent. On this aspect there is a short transverse suture extending from below the the lateral margin of the maxilla, attachment of the maxillary palpus, which is a continuation of the suture on the caudal aspect separating the galea and palpifer. On the cephalic aspect this suture separates the galea from the stipes for a short distance. On this aspect, too, the galea, which is covered with long setae, is separated from the part of the maxilla mesad of it, the lacinia, by a distinct suture.

Lacinia (Pl. XX):- The lacinia is the large lobe lying on the cephalic surface of the maxilla. On this aspect the galea is laterad of the lacinia, but the larger part of the galea, which is on the caudal surface of the maxilla, is caudad of it. It is separated from the stipes and galea on its lateral margin by a distinct suture, which near the angle of the maxilla turns mesad at a right angle, soon becoming obsolete, so that for a part of its proximal margin the lacinia is fused with the sclerite proximad of it, the stipes. The



lacinia is densely covered with the large, heavy setae which characterize the galea. The distal end, which does not extend quite as far ventrad as the tip of the galea, is broadly rounded and bears three heavy teeth which point mesad.

LABIUM (Pl. XXI):- The labium is a comparatively small lobe attached to the distal margin of the gula. Along it's lateral margins the hypopharynx is attached to it and forms with it the lower lip.

Submentum (P1. XXI):- The submentum comprises over half of the entire labium, being as wide as the distal margin of the gula, but only one-half as long. It is united with the superlinguae along its lateral margins. The proximal half is more heavily chitinized than the distal half. On each side of the meson between the proximal and distal margins there is a long, heavy seta which projects nearly to the distal end of the labium.

Mentum (Pl. XXI):- There is no trace of any mentum in this insect. In Corydalis it is a small sclerite which is entirely covered by the submentum. In the carabid it is extremely minute. If there is any portion of it left, and this is doubtful because of the greatly reduced size in other forms, it is completely fused with the submentum.

Ligula (P1. XXI):- The ligula is the distal part of the labium attached to the submentum. It is broadly rounded, and the lingua is attached to it on it's lateral and distal margins. The greater part of the ligula is heavily chitinized.



This chitinized area is in the form of a band which extends from the lateral margins of the ligula to the meson, where it projects ventrad. As the lateral margin is expanded on each side, there is a deep emargination on each side of the distal margin of the chitinized band. There is a single seta on the distal margin in each of the proximal angles of the median projection.

Palpigers--Labial Palpi (Pl. XXI):- The labial palpi are inserted in the deep emarginations of the chitinized part of the ligula. The palpifer is fused with the other parts of the ligula without any indication of a suture. Each labial palpus is a short, two-segmented appendage. The first segment is as broad as long. The second is longer and more narrow, tapering slightly to a broadly rounded point which is covered with tiny cone-shaped organs of special sense.

Paraglossae and Glossae (Pl. XXI):- The paraglossae and glossae are not distinct, but are entirely fused with other parts of the ligula.

PROPHARYNX AND HYPOPHARYNX:- In this beetle both the propharynx and the hypopharynx are well developed along lines which tend to increase the efficiency of the crushing and grinding apparatus. There is a much greater differentiation of parts than in either of the forms previously studied.

Propharynx (Pl. XXII):- In the carabid the frontal lobe, epipharynx, and fulcrum are not differentiated. In Corydalis the fulcrum is well developed, but there is no indication of



an epipharynx. In Xyloryctes, the propharynx is differentiated into these three component parts. From the opening into the pharynx, which is just dorsad of the fronto-clypeal suture, the dorsal wall proceeds ventrad as a thin, wide, cuticular membrane, lining the clypeus, to the clypeo-lateral suture where it becomes more heavily chitinized and lines the labrum. It is closely applied to the ental surface of this sclerite, and is attached to its lateral and ventral margins.

Frontal Lobe (Pl. XXII): - The frontal lobe is the part of the propharynx that lines the labrum. It is membranous and broadly oval in out-line. Along the distal margin there is a more heavily chitinized ridge which is produced dorsad near the meson into a bluntly triangular tooth-like projection which is to the right of the meson. Along the lateral margins this ridge is hyaline and bears a row of long, heavy setae which point disto-mesad and project beyond the distal margin of the labrum. These are constricted at their base and fit indeep sockets formed by the outfolding of the cuticle. The median projection of this ridge does not bear any setae, is more heavily chitinized, and is dark brown in color. There is an emargination in the distal margin of this chitinized area which is like the lateral portions of the ridge and which bears two long setae. It is only the median brown projection that is seen in unmounted specimens, in which it appears as a single median tooth.

Proximad of this tooth there is a central clear area ex-



tending to the proximal margin of the frontal lobe. Laterad of this, there is on either side an area covered with sharply pointed setae which point mesad and which decrease gradually in size from the meson laterad. The setaceous area does not extend to the lateral margin.

Fulcrum (P1. XXII):- The fulcrum is asymmetrical. On the right side it extends from a point two-thirds of the distance between the lateral margin of the propharynx and the meson, laterad, around the lateral margin to a point near the lateral end of the ridge of the frontal lobe. It is a narrow, very heavy, thick, chitinized, curving bar. On the left side it extends transversely from a point a little farther mesad than that on the right side, as a straight chitinized rod, to the lateral margin of the frontal lobe, where it terminates. The mesal end of this half of the fulcrum is bluntly forked.

Epipharynx (Pl. XXII):- Between the mesal ends of the halves of the fulcrum there is a longitudinal rod of the same length as the right half of the fulcrum, which projects proximad from this point. The ventral end of this rod is slightly dilated and on it are four sensory pits. It seems probable that this is the epipharynx. There are three other areas of chitinization in the proximal membranous part of the pharynx near the frontal lobe. One is a small, transverse bar proximad of the right half of the fulcrum. The second is a small, slightly chitinized spot proximad of the first, while the third is a small spot on the left side, proximad of the ful-



Between this area of chitinization and the left half of the fulcrum there is a small group of sharp, triangular setae which are directed mesad. Proximad of this, the propharynx is non-setaceous. Professor George H. Carpenter, of the Royal College of Science, Dublin, in a paper on the mouth-parts of some beetle larvae which was published in the Quarterly Journal of Microscopic Science, 1912, describes the mouth-parts of a larva of Geotrupes. He figures the fulcrum and epipharynx as posterior sclerites of the labrum. He is not consistent, however, for in the text he describes the tooth of the frontal lobe as being part of the epipharynx. This is impossible if the sclerites proximad of it are a part of the labrum. Moreover, when the propharynx and hypopharynx are removed the sclerites are seen to be part of the propharynx and are not associated at all with the labrum, which is a single, homogeneous, flat sclerite.

Hypopharynx (Pl. XXII):- From the opening into the pharynx, the hypopharynx extends ventrad as a narrow, membranous band for about the same distance as the propharynx. At a point entad of the dorsal margin of the frontal lobe it is slightly broadened, but at no point is it's width equal to that of the frontal lobe. This proximal part is a thin cuticular, nonsetaceous membrane which is joined to the mesal margins of the basal portion of the maxillae and to the lateral margins of the gula.

Lingua (Pl. XXII):- The terminal lobe-like part of the



hypopharynx is the lingua. It is only as wide as the walls of the pharynx, and is as long as broad, lying entad of the ligula and forming with it the terminal portion of the lower lip.

The lingua is fused on it's lateral margins with the expanded margins of the elevated chitinized band of the ligula, and on its ventral margin with the region of the labium that probably represents the fused glossae and paraglossae. The dorsal margin is deeply convex, fitting into the concave ventral margin of the superlinguae, which are, as in Corydalis, fused on the midline, completely separating the lingua from the proximal part of the hypopharynx. The lingua is covered with setae, those near the proximal margin being short, thick, bluntly pointed and directed proximad towards the pharyngeal opening. Those on the distal half are long, more slender and pointed mesad.

Opening of the Salivary Ducts (P1. XXII):- The salivary ducts meet in a common median duct underneath the proximal part of the hypopharynx. This short duct opens into the mouth-cavity on the meson near the dorsal margin of the lingua. This opening may be plainly seen in mounted specimens, and the ducts traced by dissection.

Superlinguae (Pl. XXII):- The superlinguae show the most peculiar development of any part of the hypopharynx. They fuse on the meson entad of the submentum, forming a broad, heavy band separating the lingua from the proximal part; of the hypopharynx. The distal margin is concave on the meson. The distal angles are broadly rounded from this concavity to the



broadest point of the band, which is half way between the dorsal and ventral margins. From this point on each side the lateral margin extends obliquely meso-dorsad to the ventral angles of the narrow membranous part of the hypopharynx. The dorsal angles of the superlinguae are produced a short distance dorsad of the dorsal margin, which is straight, along the lateral margins of the proximal part of the hypopharynx. The right side of the band, laterad of the meson, is produced into a large, heavy tooth which projects distad and cephalad over the lingua and fits against the molars of the mandibles, assisting in closing the buccal cavity and making a more perfect molar apparatus. On each side of the superlinguae there is a thin, membranous area, in the center of the broad, shoulder-like side. This area is much larger on the left side than on the right where the tooth is located.

On this oval area, on the left side, there is a row of short, broad, solid setae arranged in a semi-circle, which are pointed toward the meson. The ventro-lateral angles of the shoulders on both sides are covered with long, pointed setae, of the same description as those on the distal margin of the propharynx. The broad band, which seems to be the fused superlinguae, Professor Carpenter figures as being composed of what he terms a transverse sclerite and two lateral acterites, with no attempt at an interpretation of their homologies. The superlinguae (maxillulae of Carpenter) he confines to the clear spaces on the lateral prominences. This seems to be a



rather forced homology, for it leaves the greater part of this region unaccounted for. In the light of the condition found in Corydalis, where the superlinguae are fused, there is no doubt but that the entire structure is superlingual in origin.

Pharyngeal Sclerites (Pl. XXII):- There is on each side of the hypopharynx, extending from half-way between the band of the superlinguae and the pharyngeal opening an irregular, light-brown piece. These extend a short way proximad of the pharyngeal opening, along the lateral margins of the pharynx. They are the pharyngeal sclerites, and serve as a support for the walls of the pharynx.



V. LEPTINOTARSA DECEMLINEATA

There is in this form a modification from the type found in the carabid owing to the fact that the mouth opening is directed ventrad instead of cephalad. This is not a more generalized condition, for it is a secondary development from the carabid type. In the more generalized beetles there has been a cephalic rotation of the head with the consequent development of a gula. In certain beetles the head is rotated secondarily caudad, so that the mouth opening is directed ventrad. This shortens the distance very much between the occipital foramen and the mouth-parts. The genae are shortened, and the gula, which is very long in both the larva of Corydalis and the carabid larva, is secondarily reduced to a broad, narrow membrane between the occipital foramen and the labium. It is so much reduced, in fact, that the labium is practically attached directly to the cervical membrane at the margin of the occipital foramen and approaches very closely to the condition found in generalized insects in which there has been no rotation of the head.

FIXED PARTS OF THE HEAD

The fixed parts of the head are more highly specialized than in either of the beetles previously studied. The head capsule is more completely fused, and the tentorium more highly developed.

Epicranial Suture (Pl. XXIII): - The entire head is short,



round, and small. On the cephalic aspect the epicranial suture extends ventrad on the meson from the margin of the occipital foramen to about one-third of the distance between the margin of the head and the fronto-clypeal suture where it divides widely, the two branches extending directly toward the antennal sockets, but becoming obsolete a short distance mesad of the insertion of the antennae. There is a line extending the entire length of the meson between the occipital foramen and the clypeus, This is not a suture, however, but a furrow marking the attachment on the ental surface, of a dorsal projection from the frontal plate of the tentorium.

Vertex (P1. XXIII):- The vertex is the region on either side of the epicranial suture. It extends ventrad from the dorsal margin of the head, laterad of the epicranial suture, to the ventral margin of the head capsule. Ventrad of the point where the epicranial suture becomes obsolete, the vertex is fused with the front. In the light of conditions found in other forms, it is probable that the region on each side which bears the ocularium and antennal socket is a part of the vertex. The vertex extends around onto the caudal aspect of the head where it is fused with the gena on each side without indication of a suture. The antennal socket is situated on the lateral aspect of the head at the cephalic margin of the head capsule and is visible from both the cephalic and caudal aspects. The ocularium is the region of the vertex on each side dorsad of the antennal socket. There are six simple



eyes. Four of these are arranged in the shape of a diamond.

One is at the dorso-lateral angle of the antennal socket,

another at the ventro-lateral angle. Just ventrad of the latter the dorsal arm of the tentorium is attached to the ental
surface of the head.

Front (P1. XXIII):- The fwont is the triangular piece enclosed between the arms of the epicranial suture. On the dorsal two-thirds of its extent it is separated from the vertex by the arms of this suture. The ventral third is fused with the vertex. It extends ventrad to the fronto-clypeal suture, which extends between the invaginations of the anterior arms of the tentorium. This is different from the condition in the larva of Corydalis or the carabid larva where the fronto-clypeal suture is entirely obsolete.

Clypeus (Pl. XXIII):- The clypeus is the sclerite ventrad of the front, which is three times as broad as long.

There is no indication of a suture dividing it into a first and second clypeus. There are four clypeal setae on each half, two of which are on the lateral margin, one dorsad of the other.

The antecoxal pieces of the mandibles are completely fused with the clypeus, so that a mandible articulates against each dorso-lateral angle of the clypeus.

Trochantin of the Mandible (Pl. XXIII):- Although the antecoxal piece of the mandible which is typical of generalized forms is fused with the clypeus, there is present another sclerite which indicates a generalized condition. This is the



trochantin of the mandible, which was not present either in Corydalis of the carabid. It is a small, crescent-shaped sclerite on each side of the head between the dorsal and ventral articulations of the mandible, which separates the mandible from the gena and vertex. On the cephalic aspect, it extends mesad to a point ventrad of the mesal margin of the antennal socket, and extends on the ventral side to the condyle of the gena for the articulation of the mandible. This sclerite is supposed by Comstock and Kochi to be homologous with the trochantin of a thoracic leg which is a small piece lying in the membrane between the two articulations of the coxa.

Labrum (P1. XXIII):- The labrum is the flap at the ventral edge of the clypeus. It is about twice as long, but narrower than the clypeus. The angles are broadly rounded, and there is a deep rounded emargination at the middle of the ventral margin. This is a typical lepidopterous character which is closely correlated with the leaf-eating habits of this beetle. There are five pairs of labral setae. The dorso-lateral angles are produced into sharp, triangular projections which extend dorsad, entad of the clypeus. The mandibles rest against these projections and the propharynx is attached to them.

Genae (Pl. XXIII):- There is very little of the head capsule visible on the caudal aspect of the head, due to the ventral position of the mouth. The mouth-parts have been drawn back so that there is practically no space between the occipital foramen and the labium. Laterad of the labium, the head capsule is shortened, and much of this part is covered by



the membrane of the neck, which widens out immediately dorsad of the labium to almost the entire width of the head covering all the postgenae and part of the genae.

The genae occupy more than half the caudal aspect of the head. Near the lateral margin of this aspect the genae are fused with the vertex, which extends to the caudal aspect of the head and on which occur the antennal sockets and the ocularium, most of which are visible from the caudal aspect.

Each gena is separated from the sclerite mesad of it, the postgena, by a distinct suture extending from the ventral margin of the head directly dorsad, which becomes obsolete shortly before reaching the occipital foramen so that for a short distance the gena and the postgena are fused.

Mesad of the trochantin of the mandible, the gena is produced ventrad in a triangular projection, at the apex of which there is an acetabulum for the reception of the ventral condyle of the mandible.

Postgenae (P1. XXIII):- The postgenae are situated mesad of the genae, between the genae and the occipital foramen. In general, they are triangular in out-line, the three sides being bounded by the ventral margin of the head, the genal suture, and the margin of the occipital foramen. They are fused only a short distance with the genae where the dorsal ends of the genal sutures have become obsolete. The postgenae do not meet on the meson of the caudal aspect, but are widely separated, the space between being bridged by the body of the



tentorium. The invaginations for the posterior arms of the tentorium are pronounced slits at the meso-ventral angles of the postgenae.

Gula (Pl. XXIII): - The gula has been reduced to a broad, narrow membrane, lying ectad of the body of the tentorium, connecting the cervical membrane with the labium.

TENTORIUM(P1. XXIV):- The tentorium is much more specialized and the relation of the parts more complicated than in the carabid larva. There is a change in the relative position of the parts, which results from the great difference in the shapes of the two forms, as well as differences due to the greater development of the parts. The most notable difference is in the relation of the dorsal arms. In the larvae of both Corydalis and the carabid, the dorsal arms extend mesad on the ental surface of the dorsal side of the head and fuse with the anterior arms. In Leptinotarsa they extend mesad on the caudal aspect of the head and are associated entirely with the posterior arms.

The parts of the tentorium are all closely applied to the head capsule, there being no pillars extending through the head cavity. Externally the parts are clearly visible as ridges.

Anterior Arms (Pl. XXIV):- The anterior arms are invaginated at the dorso-lateral angles of the clypeus. The points of invagination are not definitely marked. Laterad of the clypeus each arm is expanded into a knob-like protuberance



which is situated at the ventral edge of the front, and against which the mandible articulates.

The anterior arms proceed from the lateral angles of the clypeus, mesad, along the fronto-clypeal suture, meeting on the meson where they fuse, forming the frontal-plate. In neither Corydalis nor the carabid is there the formation of a frontal-plate from extensions of the anterior arms. At the meson each arm sends off a branch. These extend, adjacent to each other, along the meson of the cephalic aspect. Just dorsad of the division of the epicranial suture they both fuse with a ventral projection of the posterior arms, which surround the occipital foramen. The dorsal branches of the anterior arms are closely applied to the head, giving it the appearance of being divided from the occipital foramen to the clypeus by a median suture.

Posterior Arms (P1. XXIV):- The posterior arms are invaginated at the mesal angles of the postgenae. The points of invagination are seen as large slits just laterad of the attachement of the labium to the gular membrane. The main part of the posterior arm of each side proceeds mesad from the point of invagination as a broad band. These fuse on the meson and make a bridge across the occipital foramen between the mesal angles of the postgenae, forming the body of the tentorium entad of the gular membrane. On each side from the ventral margin of the body of the tentorium there is a slender, tendon-like projection which folds back under the



body of the tentorium and lies along the mandibular tendon.

From the dorsal side of the invagination of each arm, there is a branch which extends directly dorsad around the occipital foramen. These two branches meet and fuse on the meson of the dorsal aspect so that the occipital foramen is surrounded by the posterior arms. From the point of fusion there is a short ventral projection, extending entad of the stem of the epicranial suture, which fuses with the dorsal projections from the anterior arms.

From the ventral side of the invagination of the posterior arm, there is a branch, more slender than that which surrounds the occipital foramen, which extends directly laterad along the ventral margin of the head capsule to the suture separating the gena and postgena. At this point it turns abruptly dorsad, extending as a slender, pointed projection the entire length of the suture, adjacent to a branch of the dorsal arm.

Dorsal Arms (P1. XXIV):- The points of invagination of the dorsal arms can not be seen externally. Each is attached on the ental surface of the ventral aspect of the head, between the antennal socket and the trochantin of the mandible. From this point it extends along the suture between the gena and the trochantin of the mandible. Near the lateral end of the trochantin of the mandible on the caudal aspect of the head it divides, one branch following the trochantinal suture ventrad to the apex of the triangular projection of the gena,



where the mandible is articulated. The other branch proceeds directly mesad to the suture separating the gena and postgena, where it turns abruptly dorsad and extends along the lateral margin of this suture adjacent to the dorsal branch of the posterior arm. Between the distal end of this suture and the apex of the genal triangle, along the mesal margin of this triangle, there is a short piece of the dorsal arm connecting these two branches of the dorsal arms.

The acetabulum at the apex of the genal triangle, into which the ventral condyle of the mandible is articulated, is formed by the dorsal arm of the tentorium. The genal triangle is entirely margined by branches of the posterior arms. This makes the whole structure more firm, and affords a more stable attachment for the mandible.

MOVABLE PARTS OF THE HEAD

The mandibles in this insect are not developed as they are in Xyloryctes, as Leptinotarsa is a leaf-eating beetle.

The labium and maxillae are connected by the buccal membrane.

The general position of these parts, however, is like that in the chrysomelid.

MANDIBLES (Pl. XXV):- The mandibles are very short, broad, and do not extend as far ventrad as either the labium or the maxillae. They are not heavily chitinized, except at the distal ends. From the cephalic aspect they appear rectangular in out-line, with the distal edge of the rectangle produced into fine, short teeth of equal size. From a lateral aspect they



are triangular in out-line. The mesal or ental surface is concave, while the lateral or ectal is convex.

The dorso-mesal angle of each mandible fits under the clypeus and rests against the dorsal projection of the proximal angle of the labrum, which extends dorsad, entad of the clypeus. It is to this mesal angle that the large mandibular tendon is attached. On the cephalic aspect at the middle of the dorsal margin there is a rounded protuberance which contains an acetabulum. This fits over the lateral protuberance of the anterior arm of the tentorium laterad of the clypeus. On the caudal side there is a long, slender prominent condyle which fits in the acetabulum formed by the dorsal arm of the tentorium at the apex of the genal triangle. The lateral margin of the mandible between the points of articulation is slightly convex, fitting into the trochantin of the mandible, which is concave on the ventral margin.

MAXILLAE (P1. XXVI):- The maxillae are soft, fleshy, lobe-like appendages on the caudal aspect of the head. The head has been rotated so that the mouth-opening is directed ventrad instead of cephalad, and the buccal parts have been drawn back so that they are attached to the gular membrane near the margin of the occipital foramen and so form the greater part of the caudal aspect of the head. In the carabid and Corydalis the mouth opening is directed cephalad, the mouth parts are attached at the end of the genae and gula, which are large and form the ventral floor of the head capsule.in these



insects. The labium and maxillae are all free appendages, but at their proximal ends are connected by folds of delicate membrane which also connects with the lateral margins of the propharynx and hypopharynx, so that it forms a part of the wall closing the buccal cavity. This is true of the adults of many biting insects. This delicate membrane, which is attached to the proximal ends of the labium, maxillae, and mandibles, may be called the buccal membrane. In the case of Leptinotarsa, where the head has been rotated and the mouthparts drawn back, if the labium and maxillae were free and unconnected there would be no closed caudal side of the head; the mouth opening would be directly into the occipital foramen. To obviate this the buccal membrane, which in the forms previously studied, merely connected the proximal ends of the mouth-parts, in Leptinotarsa is expanded and connects the lateral margins of the gula and labium with the maxillae, forming the closed floor on the caudal aspect of the head.

The maxillae are attached on the caudal side of the head to the ventral margin of the head capsule at the mesal angles of the postgenae, where there is a slight convexity, just laterad of the points of invagination of the posterior arms of the tentorium. From the mesal angle of each postgena, the margin of the occipital foramen slopes dorsad, so that the length of the head capsule increases from that point to the lateral margin of the head. Consequently, the distance between the occipital foramen and the proximal margin of the



mouth-parts is increased.

Cardo (P1. XXVI):- The cardo is the proximal sclerite of the maxilla, attached to the postgena. There is no definite articulation between them. The cardo is a shoulder-like sclerite situated mainly on the cephalic side of the maxilla. At its proximal margin it is folded over onto the caudal side in a long, slender triangle. It is attached to the postgena on the crest of this fold, near the mesal margin of the maxilla, along which the buccal membrane attaches to it.

Stipes (P1. XXVI):- The distal part; of the maxilla is a thin, flat membrane for nearly all of its extent. The stipes is by far the largest of all the maxillary sclerites. It occupies, on the caudal aspect, all the distal part of the maxilla except a slender mesal sclerite, the lacinia, and a square sclerite at the meso-distal angle of the maxilla. On the cephalic surface it comprises all the distal part except the slender mesal sclerite. It is entirely thin and membranous. At its widest point it is four times as wide as the maxillary palpus. There is a single long, extremely slender seta on the disto-lateral angle of the caudal surface. Proximad of this there are a few irregularly arranged sensory pits.

Palpifer (Pl. XXVI):- From the middle of the ventral margin of the stipes on the ventral aspect there is a fine, wavy suture which extends directly dorsad for one-fourth of the entire length of the stipes. At this point it turns mesad, at a right angle, and soon becomes obsolete. The sclerite which



is nearly completely separated from the stipes by this suture is the palpifer. It is square in out-line and is present only on the caudal surface. To its distal margin the maxillary palpus is attached.

Maxillary Palpus (Pl. XXVI):- This is the four-segmented appendage borne by the palpifer. The first segment is as wide as the palpifer at its proximal margin, but narrows to one-half that width at its distal margin. On the caudal surface there are two long setae at the proximal angle. On the cephalic side of both the first and second segments there are tiny triangular papillae pointing meso-ventrad. The second and third segments are only one-half as wide as the first and are wider than they are long. There are two setae on the cephalic margin of each of these segments. The fourth segment is longer than the second or third, and narrows to a truncate point which bears several minute cone-shaped organs of special sense.

Galea (Pl. XXVI):- The galea is a roundly pointed appendage of the same width and one-half as long as the palpus, and situated mesad and dorsad of it. Along the mesal margin of the galea there are two long and three shorter setae projecting mesad. These are all stout and heavy, and are on the cephalic surface.

Lacinia (Pl. XXVI): - Along the mesal margin of the maxilla, extending from near the cardo to the ventral margin, there is a very slender, more heavily chitinized piece. This



is connected for its entire length with the lateral margin of the labium by the buccal membrane. The distal end of this piece is extended in a very slight, blunt protuberance mesad of the galea. This sclerite is not separated from the sclerites laterad of it, the stipes and the palpifer, by a distinct suture, but the line of fusion is apparent. This piece is probably the homologue of the lacinia. The form and position of this piece are the same as in the carabid or in Corydalis, in both of which the homology was much more easily determined. In this species the lacinia is reduced considerably and is much less distinct.

Labium (Pl. XXVI):- The labium is situated on the caudal aspect of the head, mesad of the two maxillae, and together with the maxillae forms the fleshy part which occupies most of the caudal aspect of the head. It extends ventrad from near the margin of the occipital foramen, where it is attached by the broad, narrow gular membrane, mesad of the invagination of the posterior arms of the tentorium and ectad of the body of the tentorium. The labium is a flatly rounded lobe which is connected with the maxillae along its lateral margins by the buccal membrane. At the ventral end, it folds over to the ventral aspect where it fuses with the distal margin of the hypopharynx. It is on the ventral aspect of the lower lip that the two short labial palpi are borne.

Submentum (Pl. XXVI):- The labium of this insect is strikingly different from either that of Corydalis or the



carabid. In both these forms the labium was a free appendage attached to the gula, in Corydalis, or to the gular membrane in the carabid. In these forms, too, the different sclerites of the labium are more or less distinctly separated. In Leptinotarsa the submentum and ligula are fused into one general membrane. It is doubtful if the mentum is represented in this fusion at all. This sclerite was extremely minute in the carabid and in Corydalis. In Xyloryctes, a scarabaeid, there is no trace of a mentum, although the ligula and submentum are separated by a distinct suture. At the ventral end of this membrane there is a somewhat depressed area surrounded by a heavily chitinized elevation in the shape of a figure eight. This ridge is probably a secondary development for the support of the soft and fleshy labium. The elevation is interrupted on the middle of its ventral side for a short distance. Inside of this ridge the membrane is rounded up into two flat mounds with a valley between. At the proximal end of this area, just ventrad of the ridge, there is a pair of large setae. Toward the distal margin on either side of the central depression there are a few fine setae and sensory pits.

Palpigers and Labial Palpi (Pl. XXVI):- On the proximolateral part of the membranous mounds there is a short, twosegmented appendage. The first segment is short and ringshaped. There is a possibility that this is the homologue of the palpiger, but it seems more probable that the palpiger has been reduced even more than the palpifer of the maxilla and



is completely fused with the area of the ligula surrounding the palpi. The second segment is longer, narrower, and truncate at its distal end. There is a ring of extremely minute, cone-shaped organs of special sense around the margin of the truncate apex.

Paraglossae and Glossae (Pl. XXVI):- The part of the labium laterad and distad of the chitinized elevation of the ligula consists mostly of the paraglossae. Along the sides of the labium there is a long, triangular, chitinized piece distad of the elevation of the ligula. At its distal end it articulates with the expanded distal margin of the superlingua and supports the labium. Mesad of this part each paraglossa is expanded into a membranous lobe which extends nearly to the meson. These lobes are densely papillate, the blunt, triangular papillae projecting toward the center. They do not meet on the meson, but are separated by a depression, a continuation of that mesad of the palpi. This furrow probably represents the glossae, which are completely fused with the surrounding parts. The membranous lobes of the paraglossal and the glossal regions are completely fused with the vental margin of the lingua.

PROPHARYNX AND HYPOPHARYNX: (P1. XXVII):- The propharynx and hypopharynx are more developed and larger in proportion to other parts of the head than in the carabid larva, in which form the dorsal and ventral walls of the pharynx are produced for only a very short distance beyond the pharyngeal opening,



the hypopharynx extending only to the proximal margin of the submentum. In Corydalis there is greater differentiation and development, but the hypopharynx serves only as a lining of the labium. In this species, the hypopharynx is larger than the labium and forms more than one-half of the hollow lower lip.

Propharynx (Pl. XXVII):- The wall of the pharynx is divided entad of the fronto-clypeal suture. Cephalad of this point the dorsal wall widens forming a lining for the clypeus and labrum. There is no differentiation of epipharynx and fulcrum from the frontal lobe. In this respect it is more like the condition found in the carabid, for in Corydalis the fulcrum is well differentiated.

Frontal Lobe--Epipharynx (Pl. XXVII):- The combined frontal lobe and epipharynx is membranous and of the same shape as the labrum. It is narrowly emarginate at the middle of the ventral margin, with a blunt projection on each side of this emargination. On each side caudad of these projections there is a group of four sensory pits. Caudad of these pits the propharynx is covered with tiny, slender, pointed, papillate projections. In the middle these point directly caudad toward the opening into the pharynx, on the side they point mesad toward the pharyngeal opening.

Hypopharynx (Pl. XXVII):- The hypopharynx is the extension of the ventral wall of the pharynx, and forms the ental surface of the median caudal part of the head, the ectal sur-



face of which, is formed by the labium. In the carabid the hypopharynx extends only a very short distance beyond the pharyngeal opening. Here it extends to the most ventral margin of the head parts and forms a noticeable part of the lower lip.

Superlinguae (Pl. XXVII): - The superlinguae are prominent chitinized pieces extending along the lateral margin of the hypopharynx from the opening of the pharynx to the point of fusion with the labium. They lie directly entad or cephalad of the lateral thickenings of the paraglossae. They are triangular inshape, with the base at the ventral end. chitinized margins of the paraglossae and the superlinguae are are connected by a narrow, delicate, cuticular membrane. At their distal margins they articulate against each other on the ventral aspect of the head along the bases of the triangles. The labium and the hypopharynx form a hollow lobe which is supported and kept in shape by these lateral chitinizations of the paraglossae and by the superlinguae. Caudad of the pharyngeal opening the superlinguae are produced as slender spurs which lie along the wall of the pharynx, but outside of it, in the head cavity. These spurs serve as supports for the pharynx instead of the more usual pharyngeal sclerites which are thickenings in the lateral walls of the pharynx.

Lingua (Pl. XXVII): - In the carabid larva the lingua was limited to the cephalic margin of the hypopharynx at the caudal end of the ental side of the mentum. In Corydalis it ex-



tends to the caudal margin of the ligula at least, while in this form it extends to the distal end of the labium and forms the ental surface of the terminal part of the lobe where it is so completely fused with the labium that the line of separation cannot be accurately determined. The lingual lobe lies between the superlinguae and is divided into two lateral mounds by a median furrow. This furrow spreads out to the entire width of the hypopharynx caudad of the prominences in the lingua. The furrow is most sharply defined between these two lateral lobes, but extends distad through the glossal region to the middle of the depressed area of the ligula and breaks the continuity of the chitinized ridge around the depressed area. The furrow is probably for the passage of the saliva, as the salivary ducts open at its proximal end. lateral lobes of the lingua are densely papillate. Toward the lateral margins of the lobes, these papillae are much more numerous, longer, more slender and sharply pointed. They grow shorter, more blunt toward the middle, and the mesal margins are entirely glabrous. The papillae bear minute solid setae. Toward the lateral margins of the lingua the suture between the paraglossae and the lingua is distinct, but becomes obsolete toward the meson, where the linguae and the glossal region of the labium are fused without any indication of a suture.

Salivary Ducts (Pl.XXVII):- The salivary ducts are seen in mounted specimens as a pair of wavy, converging lines extending from the pharyngeal opening to the proximal end of



the furrow, which is most sharply defined at this point. The salivary ducts do not join until they empty into a common opening on the lingua.



VI. DEILEPHILA LINEATA

The size, shape and general aspect of the head of this lepidopterous larva are very like the chrysomelid. The head is round and short, the mouth opening directed ventrad, and the extent of the head capsule on the caudal aspect even smaller than in Leptinotarsa. This insect shows a higher degree of specialization than does Leptinotarsa, but the direction of the modification of the parts is the same. The general relationship of the parts of the tentorium to each other and to the head capsule is the same, but is more intricate. The relationship and relative positions of the parts of the head capsule are the same, but the trochantinal sutures are obsolete in Deilephila. The labium and maxillae are even more closely united, and the laciniae more reduced.

FIXED PARTS OF THE HEAD

The shape and positions of the sclerites of the head capsule are similar to those in Leptinotarsa. The tentorium shows a much higher degree of specialization.

Epicranial Suture (Pl. XXVIII):- The epicranial suture extends from the margin of the occipital foramen, cephalad and ventrad along the meson of the dorsal and cephalic aspects of the head for one-half the length of the cephalic aspect, where it divides. From the point of division the two branches extend directly ventro-laterad to the proximal angles of the clypeus, where they turn and proceed directly ventrad to the



ventral margin of the head capsule. The arms of the epicranial suture are fine, wavy lines. Slightly dorsad of each on its dorsal half there is a straight, more distinct line which fuses with the line of the epicranial suture on its ventral half. This line is not a suture, but a furrow, marking the attachment of a branch of the anterior arm of the tentorium on the ental surface of the cephalic aspect. The "adfrontal" sclerite of W. T. M. Forbes, or "paraclypeal" sclerite of other authors, is bounded by the arm of the epicranial suture and this furrow. Since this is not a true suture, the sclerite is not a sclerite, but a part of the vertex, the region laterad of the epicranial suture.

Vertex (Pls. XXVIII and XXIX):- The vertex, the region on the dorsal and cephalic aspects of the head, laterad of the epicranial suture, is separated from the sclerites mesad of it by the epicranial suture, but is fused on the lateral aspect of the head with the gena on each side, with no indication of a suture. The ventral margin of the vertex is deeply emarginate on the lateral aspect, the antenna being inserted in this emargination. On the ventral projection of the vertex between the insertion of the antenna and the sclerite mesad of it there are two long setae on each side.

The ocularium is located, for the most part, on the lateral aspect of the head, dorsad of the antennal socket. On each ocularium there are five simple eyes. Four of these are arranged in a semi-circle, the fifth being caudad of the cen-



ter of this semi-circle. There is a pair of tiny setae dorsad of this last eye, one ventrad of it, and another long seta between it and the semi-circle. Caudad of the ventral ocellus there is also a long seta.

Front (Pls. XXVIII and XXIX):- The front is the triangular sclerite between the arms of the epicranial suture. The base of the triangle is formed by a transverse suture extending between the arms of the epicranial suture, and separating the front from the sclerite mesad of it. The front is covered with regularly arranged setae. There is one long, thick seta on each side near the ventral margin one-fourth of the width of the front, mesad of the lateral angle of the front.

Clypeus (P1. XXVIII):- The clypeus is situated at the ventral margin of the front. It is three times as broad as long. The vertex, which extends ventrad to the middle of the lateral margin of the clypeus, is separated from the clypeus on each side by the distal end of the arm of the epicranial suture. Ventrad of the ventral margin of the vertex the lateral margins of the clypeus converge so that the transverse part of the ventral margin is narrower than the dorsal margin. There are several small, regularly arranged setae on the clypeus, and on each side there are three long setae in a longitudinal row, half way between the dorsal and ventral margins. One of these is near the lateral margin, while the second is a short distance mesad of it. The third lies half way between the lateral margin of the clypeus and the meson. The



points of invagination of the anterior arms of the tentorium may be seen as distinct slits at the dorso-lateral angles of the clypeus.

As in Leptinotarsa, there is no indication of a suture dividing the clypeus into a first and second clypeus, and the antecoxal pieces are also probably fused with it. It may be mentioned here, too, that the trochantim of the mandibles, which are present as distinct sclerites in both the larvae of Leptinotarsa and Xyloryctes, are not distinct. On each side the suture between the trochantin of the mandible and the head capsule has probably become obsolete so that the trochantin of the mandible is fused with the vertex and gena.

Labrum (Pls. XXVIII and XXIX):- The labrum is the flap attached at the ventral margin of the clypeus. It is as wide as the transverse part of the ventral margin of the clypeus, and as long as this sclerite. The lateral margins are broadly rounded, and there is a broad, shallow emargination at the middle of the distal margin. A little less than half way between the dorsal and ventral margins of the labrum there is on each side a row of three long setae. There is one adjacent to the lateral margin, a second is located one-fourth of the width of the labrum mesad of this, while the third is near the meson. There are four setae on each side on the ventral margin between the lateral margin and the emargination. One is adjacent to the lateral margin, one is just laterad of the emargination, and there are two short, fine setae between these



two.

Genae (Pl. XXVIII):- As the occipital foramen in this insect is very large and as the mouth-opening is directed ventrad, there is very little of the head capsule on the caudal aspect. The larger part of this is occupied by the genae, which on this aspect are irregularly rhomboidal in outline. On each side the gena extends from a point half way between the meson and the lateral margin of the caudal aspect, onto the lateral aspect of the head where it fuses with the vertex, with no indication of a suture. There is an acetabulum at the meso-ventral angle of the gena which is formed by the tentorium, inwhich the caudal condyle of the mandible articulates. The genae are separated from the sclerites mesad of them, the postgenae, by short, distinct sutures extending from the occipital foramen to the ventral margin of the head capsule.

Postgenae (Pl. XXVIII):- The postgenae are the sclerites mesad of the genae. They are triangular in out-line, the apex of each triabgle being directed toward the meson of the ventral aspect of the head where the two postgenae are closely approximated, but not united. The maxillae are articulated with the postgenae, but there is no definite point of articulation.

TENTORIUM: - The tentorium of this insect is very complicated and highly specialized, with an intricate relationship between the different parts. The general line of modification is the same as that of Leptinotarsa.

Anterior Arms (Pls. XXIX and XXX): - The anterior arms are



invaginated in distinct slits at the dorso-lateral angles of the clypeus. From the point of invagination on each side there is a short, buttress-like projection which forms a knob, entad of the meso-ventral angle of the vertex, against which the mandible articulates on the cephalic aspect. There is another branch which extends mesad from the point of invagination along the fronto-clypeal suture, closely applied to the ental surface of the head. The two branches meet and fuse on the meson, forming the frontal plate of the tentorium. The third and largest of the branches of the anterior arm projects mesodorsad. They are not directly applied to the head capsule, but are attached by a narrow, vertical plate to the ental surface. The two branches meet on the meson ventrad of the point of divergence of the arms of the epicranial suture. From this point they extend as a fused plate dorsad along the meson of the cephalic aspect to a point near the margin of the occipital foramen. As this plate extends dorsad it descends farther into the head cavity, so that the single median vertical plate which connects it with the ental surface of the head capsule is increased in size. Near the occipital foramen this plate divides, each part diverging from the meson and extending to the margin of the occipital foramen. The median connecting plate is also split, half of it connecting the meson of the ental surface with the diverging plate of each side. From the point on each side where the plate reaches the occipital foramen, it extends, closely applied to the head capsule,



around the dorsal and lateral margins of the occipital foramen, extending a short distance along the ventral margin where it terminates in a small, knob-like protuberance.

From the middle of the branch of the anterior arm, extending between the dorso-lateral angle of the clypeus and the meson, on each side, there is a slender branch given off which proceeds directly caudad through the head cavity and fuses with a cephalic branch of the posterior arm.

It is the attachment of the vertical plate attaching this branch of the anterior arm to the ental surface of the head capsule on each side, extending from the dorso-lateral angle of the clypeus to the ental surface of the cephalic aspect, that forms the suture-like furrow which forms the dorsal boundary of the so-called "adfrontal" sclerite.

Posterior Arms (Pls. XXIX and XXX):- The posterior arms are even more complex in their structure than the anterior arms. They are invaginated on each side at the ventral margin of the occipital foramen, at the dorsal end of the suture between the gena and postgena. From the point of invagination there is a strong branch which follows the suture to the ventral margin of the head where it is enlarged to form, on the meso-ventral angle of the gena, a deep acetabulum for the reception of the caudal condyle of the mandible. Another branch extends mesad from the point of invagination along the dorsal margin of the postgena to the meson. The branches from the two sides do not quite meet on the meson. From the mesal



end of the invagination, there is a slender branch which extends cephalad into the head cavity and fuses with the caudal branch of the anterior arm, so there is on each side of the head a slender pillar extending through the head cavity. On each side, from the mesal margin of this branch near its point of origin there is a very fine branch which extends mesad. The two unite on the meson, forming the body of the tentorium, which divides the occipital foramen into two parts. Laterad of the point of invagination the posterior arm on each side widens out into a thin, oval, membranous plate which extends along the margin of the occipital foramen, laterad to the point where the anterior arm terminates in a knob-like protuberance.

Dorsal Arms (Pls. XXIX and XXX):- In this insect the dorsal arms are not well developed and are of little importance. On each side the dorsal arm is attached to the ental surface of the head capsule between the ocularium and the antennal socket, but the point of attachment is not apparent on the ectal surface. From this point each arm follows the margin of the antennal socket around to the caudal aspect of the head, where it proceeds directly mesad along the ventral margin of the head capsule to the meso-ventral angle of the gena, where it unites with the ventral branch of the posterior arm and forms the acetabulum for the reception of the caudal condyle of the mandible.

MOVABLE PARTS OF THE HEAD



MANDIBLES (Pl. XXXI):- The mandibles of this insect are short, and nearly as broad as they are long. They are on the cephalic aspect of the head, extending from the lateral margin to the meson of the cephalic aspect. The mesal margins are produced into short, triangular teeth. The dorsal teeth are smaller, and the larger ones are ridged on the ental surface. The largest tooth is situated at the middle of the mesal margin.

Each mandible is articulated at the latero-cephalic margin of the clypeus. There is a large condyle which is hollowed out to form a shallow acetabulum which fits over the buttress-like, lateral projection of the anterior arm of the tentorium, under the angle between the vertex, the front, and the clypeus.

On the caudal aspect of the mandible there is a globular, very prominent condyle, constricted at the base, which fits into the acetabulum which is formed by the posterior and dorsal arms of the tentorium at the meso-ventral angle of the gena. This makes a more stable articulation than if the gena were simply emarginate, and not supported by the heavily chitinized tentorium.

MAXILIAE (P1. XXXI):- The maxillae are fleshy, lobe-like organs situated on the caudal aspect of the head, laterad of the labium. They are closely united by the buccal membrane along their mesal margins, to the labium, and form with it the floor of the caudal aspect of the head. The general form of the labium and maxillae is very like that of the chrysomelid



beetle. The maxillae are twice as long as broad and extend slightly farther ventrad than the labium. The maxillae are articulated against the postgena, but there is not a definite point of articulation, the condyle of the proximal sclerite of the maxilla simply resting against the ventral margin of the postgena.

Cardo (Pl. XXXII): - The proximal sclerite, the cardo, is a small, heavily chitinized piece situated at the dorso-mesal angle of the maxilla. On the ventral aspect of the maxilla it appears roundly triangular in out-line, the apex of the triangle being directed ventrad and fitting between the dorsolateral angle of the labium and the distal part of the maxilla. The articulation of the cardo with the postgena is not visible, as the condyle is on the cephalic surface of the cardo. From the cephalic or ental aspect of a mounted preparation the ental surface of the cardo may be seen with the cephalic fold at the dorsal margin. This fold is bluntly pronged. The shorter arm extends dorsad from the middle of the ridge, forming the bluntly rounded condyle which rests against the postgena. The longer prong extends mesad and articulates with the chitinized dorso-lateral angle of the submentum on its cephalic surface.

Stipes (Pl. XXXII):- The stipes is the largest sclerite of the maxilla. It is entirely membranous, hyaline, and situated for the most part on the caudal aspect of the maxilla. It extends from the lateral margin of the cardo laterad to the



lateral margin of the maxilla, the dorsal margin being connected with the ventral margin of the postgena by the buccal membrane. This margin is curved ventrad so that the dorso-lateral angle is ventrad of the cardo.

It extends from the dorsal margin of the maxilla ventrad to the distal end of the maxilla. The lateral margin has a deep indentation one-fourth of the distance between the dorsolateral and ventro-lateral angles of the stipes. Along this margin the stipes folds over to the cephalic aspect where it fuses with the hypopharynx, which lines the larger part of the cephalic surface of the maxilla. At the distal end, cephalad of the maxillary palpus, the cephalic fold widens ventrad of the hypopharynx to the entire width of the maxilla, which narrows toward the distal end and bears the galea at its ventral margin. The cephalic fold is also widened at the point of indentation in the lateral margin. On the dorsal half of the caudal surface of the maxilla, there are several irregularly arranged setae, but the cephalic aspect is glabrous. There is a single long, slender seta which projects laterad, dorsad of the suture separating the stipes and palpifer.

Palpifer (Pl. XXXII):- The palpifer lies entirely on the caudal surface of the maxilla. There is a fine, line-like suture extending laterad from a point on the mesal margin of the maxilla, three-fourths of the distance between its dorsal and ventral margins. This suture becomes obsolete before reaching the lateral margin, so that the palpifer is fused with the stipes on the lateral quarter of its proximal margin and on



its lateral margin. Ventrad of this suture near the lateral margin of the caudal aspect there is a pair of long setae.

Maxillary Palpus (Pl. XXXII): - The maxillary palpus is a four-segmented appendage borne at the ventral margin of the palpifer on the caudal aspect of each maxilla. The two proximal segments are dorsad of the ventral margin of the cephalic surface of the stipes, so that they lie caudad of and closely applied to the ental surface of the cephalic aspect of the stipes. The first segment is as braod as the ventral end of the maxilla, and short. It is longer on its mesal than lateral surface. The proximal half is chitinized, the distal half is membranous, and there is a single very long seta half way between the proximal and distal margins. The second segment is nearly as broad as the first. The mesal surface is very short, while the lateral surface is long. On the short mesal surface of the second segment there is a moderately long setae pointed mesad. The third segment is much narrower and no longer than broad. The fourth is very short and narrowed to a truncate point which is covered with tiny coneshaped organs. Poth the distal segments are glabrous.

borne at the narrow distal margin of the stipes on the cephalic aspect of the maxilla cephalad of the third segment of the palpus. It is short, broad, barrel-shaped and pointed meso-ventrad. The surface adjacent to the palpus is chitinized, but the cephalic surface is a delicate, cuticular mem-



brane, densely covered with short, triangular papillae.

The distal end is broad and slightly concave, and on it are two short, cone-shaped organs. These are each composed of two segments, the second being an extremely minute, hardly perceptible, round tip. Adjacent to the mesal margin of the cephalic surface there are three long, strong, setae which are pointed meso-ventrad.

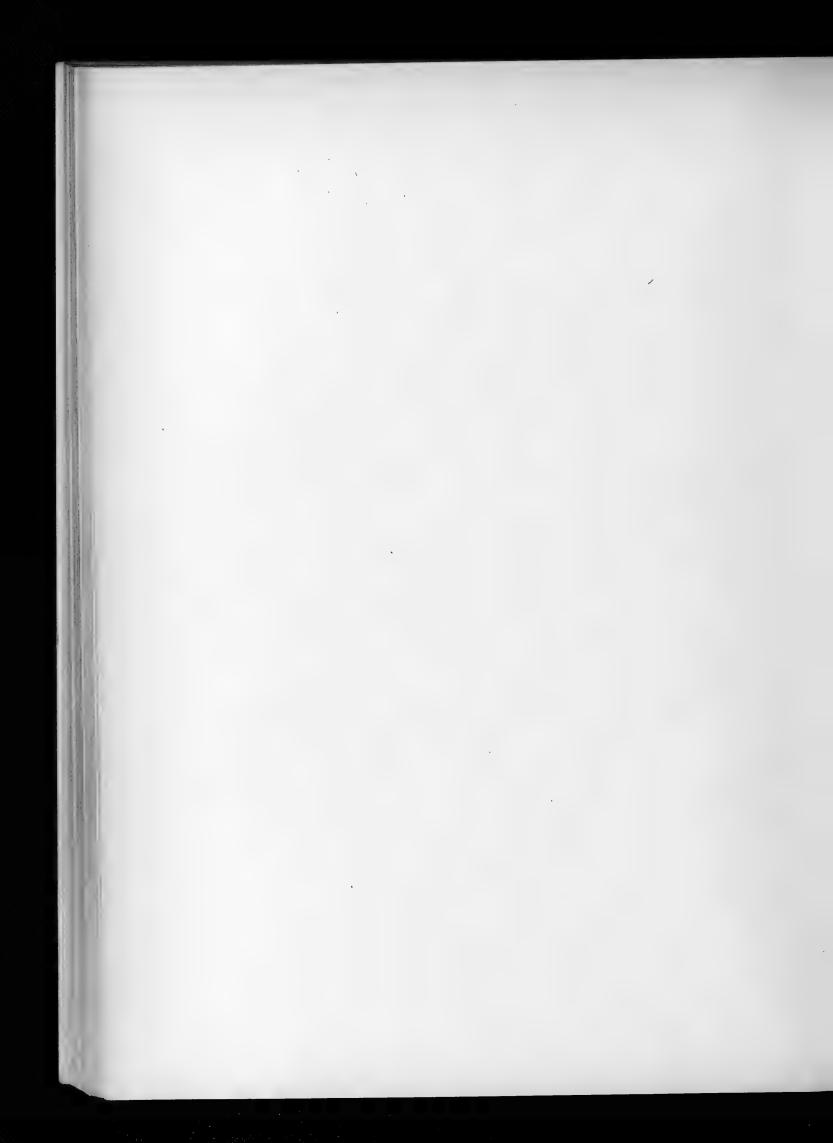
Lacinia (Pl. XXXII): - The locinia is even more greatly reduced in size than in the chrysomelid larva, but the position is the same as in all the forms previously studied. The slender, chitinized band which extends from the cardo along the mesal margin of the stipes to the point of origin of the suture separating the palpifer and stipes bears little resemblance to a lacinia, but the position and size indicate that this is the much reduced lacinia. It is visible on both the cephalic and caudal aspects as far ventrad as the point of origin of the suture between the stipes and palpifer, but ventrad of this point it turns cephalad and is only apparent from the cephalic aspect, on which aspect it follows the converging mesal margin of the maxilla to the proximal margin of the narrow distal end of the stipes ventrad of the hypopharynx, which extends between the stipes and lacinia from the cardo ventrad to a point cephalad of the proximal margin of the maxillary palpus.

LABIUM (P1. XXXIII): - The labium of Deilephila is on the caudal aspect of the head and extends ventrad from the margin



membrane to the ventral margin of the head. The form of the labium is very like that of the chrysomelid beetle. The sclerites are indistinct, and it is attached along its lateral margins to the mesal margins of the maxillae. Like Leptinotarsa, the entire lower lip is a fleshy, hollow, tubular organ formed by the labium and the hypopharynx, which are fused on their ventral margins. The whole lip is supported by a chitinized structure composed of different parts of the two organs.

Submentum and Ligula (Pl. XXXIII): - The submentum and ligula are fused. The greater part of the structure is soft, cuticular membrane. The dorso-lateral angles, which articulate with the cardines of the maxillae, are chitinized. W. T. M. Forbes, in his paper on the "Structural Study of Some Caterpillars", homologizes these angles with the submentum and calls the rest of the membranous structure the mentum. This interpretation is impossible when considered in the light of the evidence given by the condition found in more generalized forms. Even in Corydalis the mentum is much reduced, and in Xyloryctes and Leptinotarsa it is probably completely atrophied, so that it is extremely improbable that it would comprise such a large part of the labium in so highly a specialized insect as Deilephila. In the second place, in the more generalized insects studied the submentum is always large, well developed, and never divided. It is unlike-



ly that it is so greatly reduced and divided in this insect.

This cuticular part of the fused submentum and ligula extends nearly to the ventral margin of the labium. There is on each side of the meson, three-fourths of the distance from the proximal margin of the maxilla to the distal end of the cuticular membrane, a single large seta, directed ventrad. Dorsad of this there are several irregularly arranged, shorter setae. Near the distal margin there is a heavily chitinized, broad band, similar to the one present on the labium of Leptinotarsa, which extends across the labium, and which is fused on its lateral margins with the distal margins of the superlinguae. The lateral margins of the labium proximad of this band are attached to the mesal margins of the maxillae by the buccal membrane. Proximad of the broad band, the labium is not attached to the hypopharynx, which is widened proximad of this point so as to line the maxillae and labium, so that there is a continuous cavity between the labium and the maxillae on the caudal surface of the structure, and the hypopharynx on the cephalic surface of the fleshy structure. Ventrad of this band there is an oval, cuticular area which fuses with the distal end of the lingua.

Palpiger--Labial Palpus (Pl. XXXIII):- The palpiger is completely fused with other parts of the ligula. The labial palpus consists of two short segments. The first is merely a semi-circle of chitin. The second is much narrower, and very short. It bears two long setae on its truncate tip, the



mesal of which is twice as long as the lateral.

Glossae and Paraglossae (Pl. XXXIII):- The glossae and paraglossae are completely fused with other parts of the ligula.

Spinneret (P1. XXXIII):- The slit through which the spinneret protrudes is located mesad of the labial palpi at the distal margin of the lingua. The dorsal margins of this slit are bordered by a tiny chitinized band. The spinneret itself, which is a specialization of the distal end of a silk duct, is a long, slender tube. It is supported on the caudal side by short lobe which is formed from the caudal side of the duct itself. The homology of the spinneret will be considered later.

PROPHARYNX AND HYPOPHARYNX: (P1. XXXIII):- The greater part of the caudal aspect of the head is composed of a large, fleshy area comprised of the labium and the two maxillae, which are attached by the buccal membrane. This is like the condition found in the chrysomelid. In this insect, however, the propharynx forms the ental surface of the labium, being attached along the lateral margins of the labium, forming a hollow, tubular tip.

In Deilephila the hypopharynx is developed to a much greater extent and lines not only the labium, but the maxillae, forming a large part of the ental surface of the caudal aspect of the head.

Propharynx (Pl. XXXIII):- The propharynx, which joins



the hypopharynx entad of the fronto-clypeal suture, expands ventrad of that point to the entire width of the clypeus, which it lines very loosely. It lines the labrum also, and is attached to the projections of the dorsal angles of the labrum, which extend dorsad entad of the clypeus. The part of the propharynx lining the labrum is covered with minute setae which project toward the pharyngeal opening except along the margins. There is no differentiation of the propharynx into a frontal lobe, fulcrum, and epipharynx. In this respect this form is as generalized as any previously studied.

Hypopharynx (Pl. XXXIII): - The hypopharynx is large, and irregular in out-line, lining a great part of the caudal aspect of the head, which is composed of the labium and maxillae. It is attached to the distal and lateral margins of the maxillae and to the labium, distad of the broad, chitinized band near the distal end, so that there is a continuous cavity between the labium and maxillae on the ectal surface and the hypopharynx on the ental surface of this fleshy structure on the caudal aspect of the head. However, as both the maxillae and the labium are membranous and as there is no chitinous structure to prevent the collapse of the two sides, this cavity is reduced to almost nothing between the maxillae and the hypopharynx. The cavity between the labium and hypopharynx is large, as there is a heavily chitinized structure composed of the chitinized transverse band of the labium, the laciniae and the superlinguae, which absolutely prevents any collapse



of the lobe. This is necessary, as the silk ducts extend through this cavity to the distal end of the lower-lip, and the flow of silk would be impeded if the two sides of the lip collapsed. Just proximad of the band of the labium the hypopharynx splits at each lateral margin of the labium. On each side the lateral portion extends ventrad from this point to the proximal margin of the dorsal surface of the stipes. The central portion extends cephalad to the distal end of the labium, and is fused with it along its lateral and distal margins.

Lingua (Pl. XXXIII):- The lingua is the median part of the hypopharynx which lines the labium. It is cuticular membrane covered, except at the distal margin, with sharp, triangular papillae directed toward the opening of the pharynx.

Near the proximal end of this median lobe there is a depressed area which is non-papillate. The part of the hypopharynx lining the maxillae is also smooth.

Superlinguae (P1. XXXIII):- The superlinguae are located laterad of the lingua. They are slender, curving bars which extend ventrad from near the middle of the lateral margin of the lingua and turn caudad near the end of the labium, fusing with the lateral margins of the chitinized transverse band of the labium. Each lacinia is directly caudad of the superlinguae and near its distal end turns cephalad and fits in the angle between the bar of the labium and the superlingua, forming an efficient prop for the soft, cuticular lower lip.



Opening of Salivary Duct: - There is no opening of the salivary duct on the lingua, as in the chrysomelid. But at the distal end of the lingua, between the lingua and the distal end of the labium, there is a large aperture through which the spinneret, which is a modification of the end of the duct of the silk gland, protrudes. Korscheldt, and Heider and Packard believe this gland to be the homologue of the functional salivary glands of the more generalized forms. This seems probable because of the position of the opening of the duct and because of the fact that there is no salivary duct opening into the buccal cavity through the lingua. The functional salivary ducts are closely applied to the mandibular tendons and open at the bases of the mandibles. Also, in some of the Hymenoptera there are many pairs of salivary glands, among the most constant of which are those which open at the bases of the mandible and through the lingua. Evidence seems to show that this homology of the silk glands of the Lepidoptera is correct, although there is no definite proof of this interpretation. The problem must be investigated by a careful study of the development of these glands.



VII. SUMMARY

The homologies of the mouth-parts of five species have been considered in this investigation, one neuropteron, three coleoptera, and one lepidopteron. As the mouth-parts cannot be successfully homologized by themselves, the fixed parts of the head, which include the head capsule and the tentorium, have in each case been homologized. The mouth-parts are the appendages of the last three head segments. Each is usually associated with a sclerite derived from the segment to which the appendage belongs. The mandibles are the appendages of the fifth segment and are articulated with the genae which are the part of this segment. The maxillae are the appendages of the sixth head segment and are usually articulated with the postgenae. The labium is composed of the two fused appendages of the last head segment and is always attached to the cervical membrane or the gula, both of which are derivatives of the last head segment. As these points of articulation remain fairly constant, a determination of the homology of the head capsule is an aid in homologizing the mouth-parts. Conversely, an interpretation of the parts of the head capsule may be verified by the articulations of the buccal parts.

The parts of the tentorium are intimately associated with the mouth-parts and often help form the articulations for the attachment of the mouth-parts.

Although the study was begun primarily as an effort to



homologize the mouth-parts, the homologies of the head capsule and the tentorium afford as much interest as those of the mouth-parts. The parts of the head capsule, tentorium, and mouth-parts are modified together. In the more specialized forms some of the sutures separating the sclerites of the head capsule are obsolete, the tentorium is more highly developed and complicated, and the mouth-parts modified. The articulations of the mouth-parts, the head sclerites, and the points of invagination of the arms of the tentorium remain fairly constant. The undivided sclerites are modified, but their position and relationship with other parts remain the same

In conclusion, it may be said that the most notable facts in the homologies of the head-parts of the larvae studied are the fundamental similarities in positions and relationships of homologous sclerites in the different larval forms and between the larval and adult forms of the same species.

POSTSCRIPT

Since the previous pages were written a carabid larva, the second form described in this paper has been bred and proves to be Pterostichus unicolor.



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IX. LIST OF ABBREVIATIONS

```
anterior arm of the tentorium
a.ar.
           antennal socket
an.s
          antecoxal piece of the mandible
ant.cx.
           body of the tentorium
bd.t.
           buccal membrane
bu.m.
           cardo
C.
cl.
           clypeus
1 cl.
           first clypeus
           second clypeus
2 cl.
           cervical membrane
cer.m.
           epipharynx
epi.
           epicranial suture
epi.s.
           front
ft.
fr.1.
           frontal lobe of propharynx
           frontal plate of the tentorium
fr.pl.
ful.
           fulcrum
           gena
8.
           galea
ga.
gl.
           glossa
           gula
gu.
           gular membrane
gu.m.
           hypopharynx
hyp.
           invagination of the anterior arm of the tentorium
in.a.ar.
           invagination of the dorsal arm of the tentorium invagination of the posterior arm of the tentor-
in.d.ar.
in.p.ar.
           ium
1.
           lacinia
la.
           labium
           labrum
lbr.
           ligula
lig.
lin.
           lingua
           labial palpus
l.p.
           mentum
m.
           mandible
man.
           maxilla
mx.
           maxillary palpus
mx.p.
           ocularium
ol.
oc.
           occiput
           occipital foramen
oc.f.
op.sa.d. opening of the salivary duct
           opening of the pharynx
op.ph.
pf.
           palpifer
           postgena
pg.
           palpiger
pag.
           pharyngeal sclerite
ph.s.
           pleurum of microthorax
p.mic.
pgl.
           paraglossa
pro.
           propharynx
           stipes
S.
```



sm. s.mic. submentum

sp.

sternum of microthorax

su.ga. su.lin. tr.man.

spinneret
subgalea
superlingua
trochantin of the mandible

v.

vertex



X. EXPLANATION OF PLATES

- Plate I. Dorsal aspect of the head of Corydalis
- Plate II. Ventral aspect of the head of Corydalis
- Plate III. Lateral aspect of the head of Corydalis
- Plate IV. Central surface of the dorsal aspect of the head of Corydalis showing anterior and dorsal arms of the tentorium
 - Fig. 2. Ental surface of the ventral aspect of the head of Corydalis showing the posterior arms of the tentorium
- Plate V.
 - Fig. 1. Lateral aspect of the tentorium of Corydalis, the lateral aspect of the head being cut away to show the interior of the head cavity.
 - Fig. 2. Cephalic aspect of the head of Corydalis with the mouth-parts removed to show the tentorium
- Plate VI. Dorsal aspect of the mandible of Corydalis Ventral aspect of the mandible of Corydalis
- Plate VII.
 - Fig. 1. Ventral aspect of the maxilla of Corydalis
 - Fig. 2. Ventral aspect of the distal end of maxilla of Corydalis in natural position.
- Plate VIII.
 - Fig. 1. Dorsal aspect of the distal end of the maxilla of Corydalis with the tip protested
 - Fig. 2. Dorsal aspect of the cardo of Corydalis showing the articulation with the postgena
 - Fig. 3. Ventral aspect of the cardo of Corydalis
- Plate IX. Ventral aspect of the labium of Corydalis
- Plate X. Ental surface of the propharynx and hypopharynx of Corydalis
- Plate XI. Dorsal aspect of the head of a carabid larva
- Plate XII. Ventral aspect of the head of a carabid larva



- Plate XIII.

 Fig. 1. Dorsal aspect of the tentorium of a carabid larva, the dorsal side of the head being removed to show the entire tentorium.
 - Fig. 2. Ventral aspect of the anterior and dorsal arms of the tentorium of a carabid larva
 - Fig. 3. Ventral aspect of the mandible of a carabid larva
 - Fig. 4. Dorsal aspect of the mandible of a carabid larva
- Plate XIV. Dorsal aspect of the maxilla of a carabid larva
- Plate XV. Ventral aspect of the labium of a carabid larva
- Plate XVI. Ental surface of the propharynx, hypopharynx, and pharynx of a carabid larva, the pharynx being slit along one lateral margin
- Plate XVII.

 Fig. 1. Cephalic aspect of the head of a larva of Xyloryctes satyrus
 - Fig. 2. Caudal aspect of the head of a larva of Xyloryctes
- Plate XVIII.

 Fig. 1. Ental surface of the cephalic aspect of the head of Xyloryctes, showing the anterior arms of the tentorium.
 - Fig. 2. Ental surface of the caudal aspect of the head of Xyloryctes showing the posterior and dorsal arms of the tentorium
- Plate XIX.

 Fig. 1. Cephalic aspect of the right mandible of Xyloryctes

 Fig. 2. Cephalic aspect of the left mandible of Xyloryctes

 Caudal aspect of the right mandible of Xyloryctes
 - Fig. 3. Caudal aspect of the right mandible of Xyloryctes Fig. 4. Caudal aspect of the left mandible of Xyloryctes
- Plate XX.

 Fig. 1. Caudal aspect of the maxilla of Xyloryctes

 Fig. 2. Cephalic aspect of the maxilla of Xyloryctes
- Fig. 1. Caudal aspect of the labium of Myloryctes
 Fig. 2. Lateral aspect of the labium and hypopharynx of
 Xyloryctes
- Plate XXII. Ental surface of the propharynx and hypopharynx of Xyloryctes



Plate XXIII. Fig. 1.	Cephalic aspect of the head of Leptinotarsa decemlineata
Fig. 2.	Caudal aspect of the head of Leptinotarsa
Plate XXIV.	
Fig. 1.	Ental surface of the cephalic aspect of the head of Leptinotarsa, showing the anterior arms of the tentorium
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Plate XXV. Fig. 1.	Ectal surface of half of the head of Leptinotarsa flattened to show the relationship of the sclerites on the lateral aspect of the head
Fig. 2.	Caudal aspect of the mandible of Leptinotarsa
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Plate XXVI. Fig. 1.	Ventral aspect of the labium and maxilla of Leptinotarsa
Fig. 2.	Cephalic aspect of the maxilla of Leptinotarsa
Fig. 3.	Distal end of labial palpus of Leptinotarsa showing the sense-organs on the tip
Plate XXVII.	Ental surface of propharynx and hypopharynx of Leptinotarsa
Plate XXVIII. Fig. 1.	Cephalic aspect of the head of Deilephila lineata
Fig. 2.	Caudal aspect of the head of Deilephila lineata
Plate XXIX. Fig. 1.	Lateral aspect of the head of Deilephila lineata
Fig. 2.	Ental surface of the cephalic aspect of the head of Deilephila, showing the anterior arms of the tentorium

Plate XXX.
Fig. 1. Ental surface of the caudal aspect of the head



of Deilephila showing posterior and dorsal arms of the tentorium

Fig. 2. Lateral aspect of the entire tentorium of Deilephila

Plate XXXI.

Fig. 1. Ectal or lateral aspect of the mandible of Deilephila

Fig. 2. Ental or mesal aspect of the mandible of Deilephila

Plate XXXII.

Fig. 1. Caudal aspect of the maxilla of Deilephila showing its relation to the labium

Fig. 2. Cephalic aspect of the maxilla of Deilephila

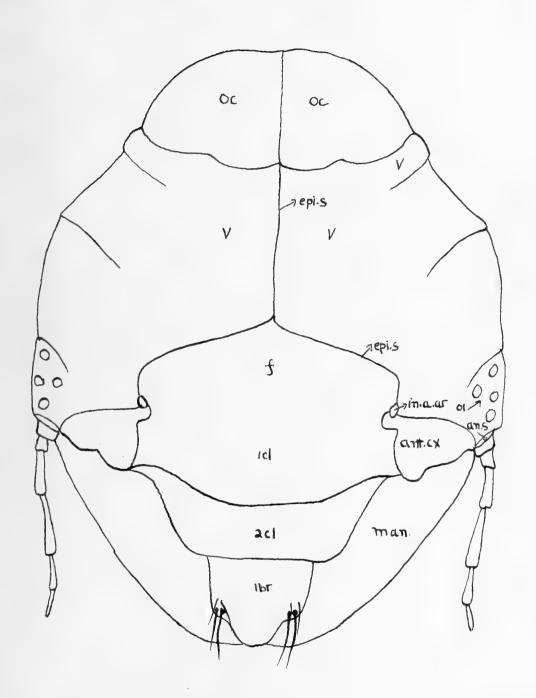
Plate XXXIII.

Fig. 1. Caudal aspect of the labium of Deilephila

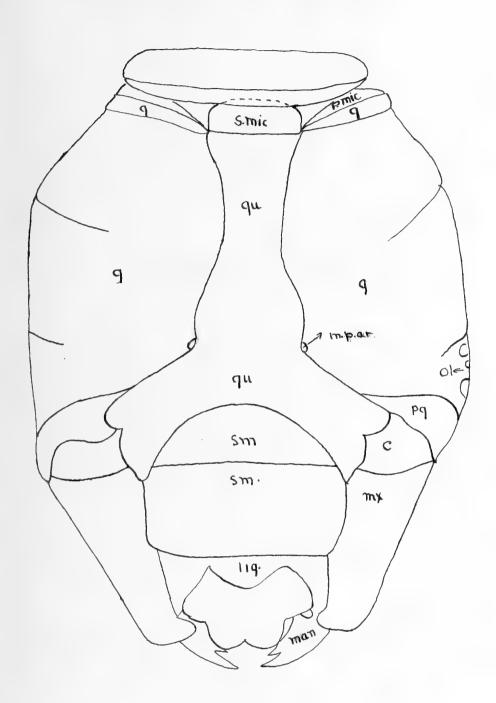
Fig. 2. Lateral aspect of a part of the ligula, the lacinia, and superlingua showing formation of the chitinized structure which supports the fleshy tip.

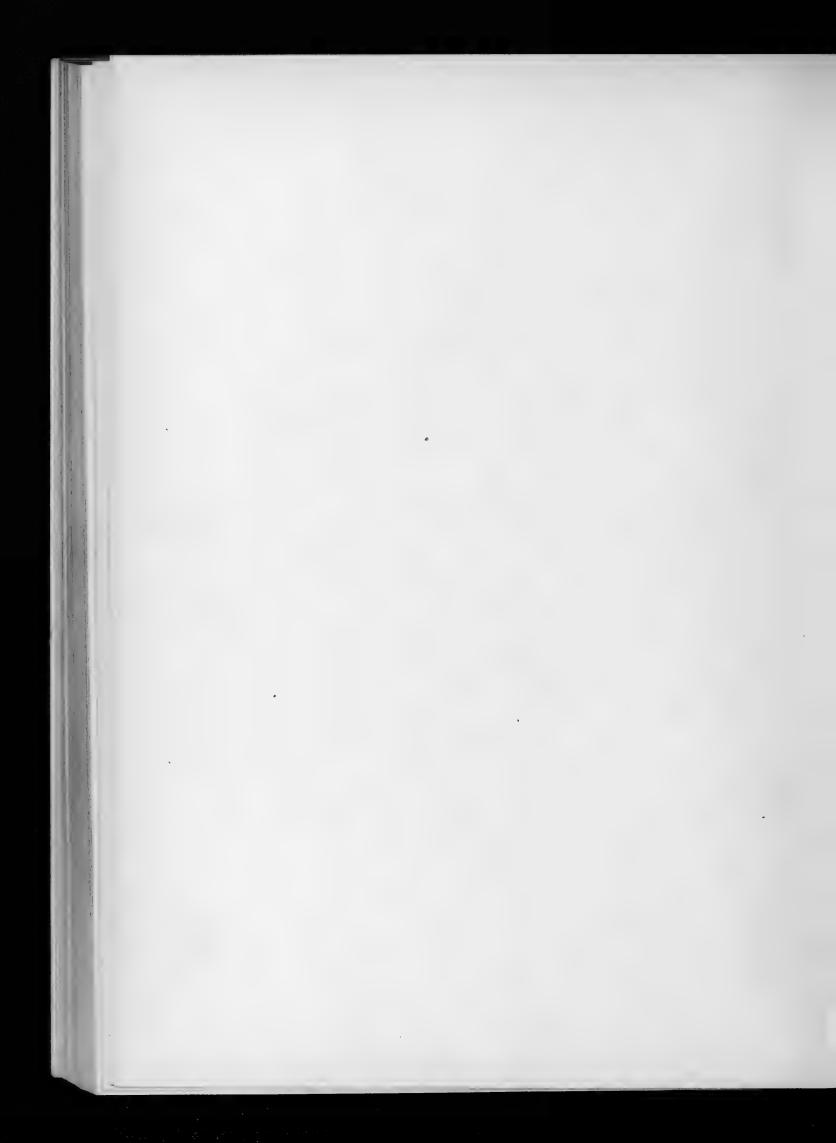
Fig. 3. Ental surface of the propharynx and hypopharynx, the pharynx being split on one lateral margin

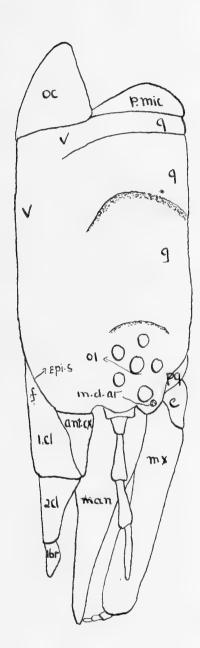




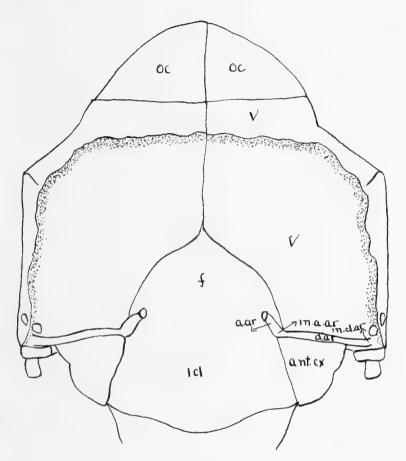




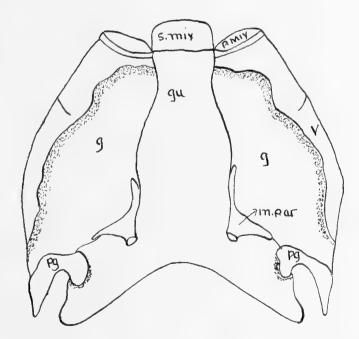








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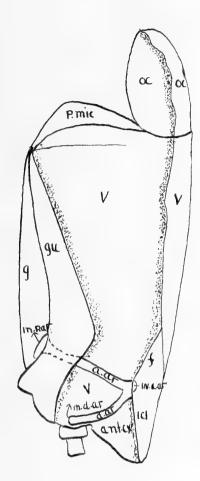


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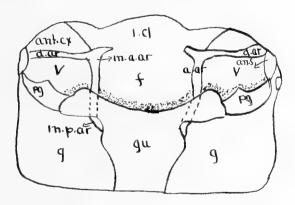
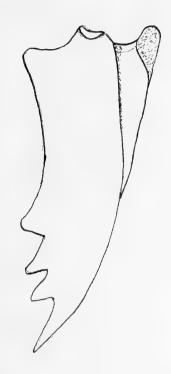


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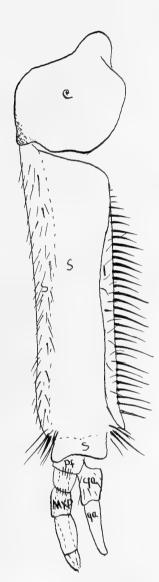




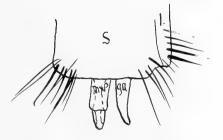
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Fig.2

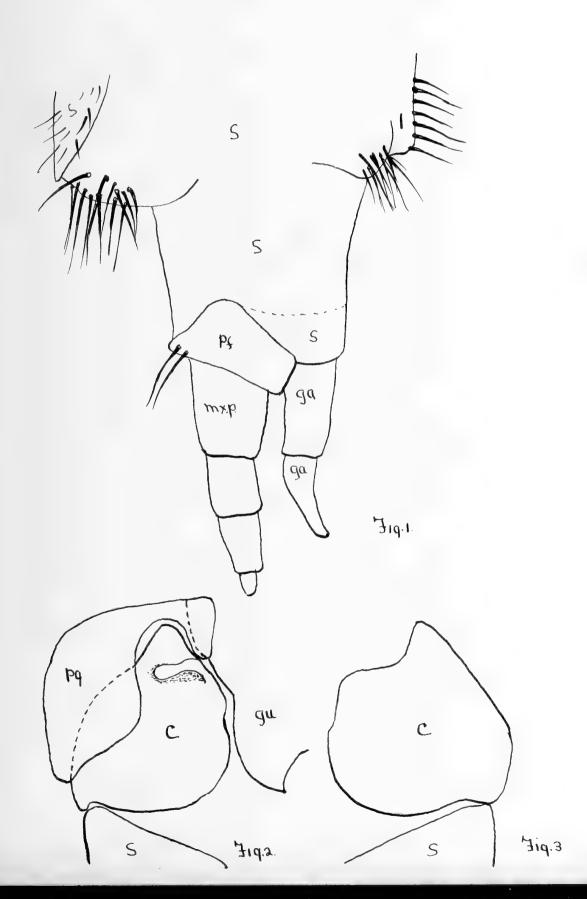


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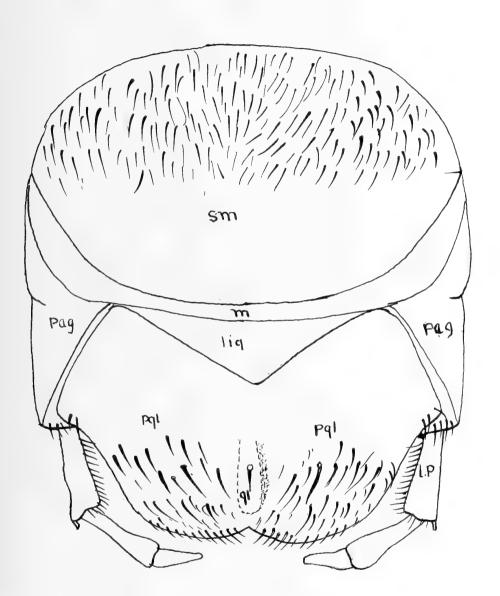


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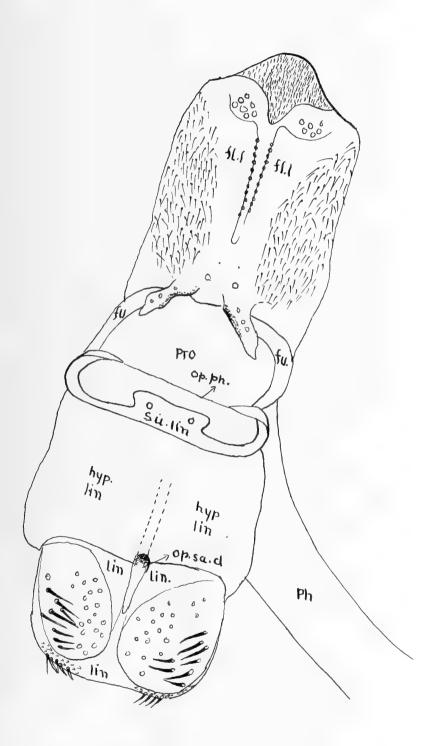




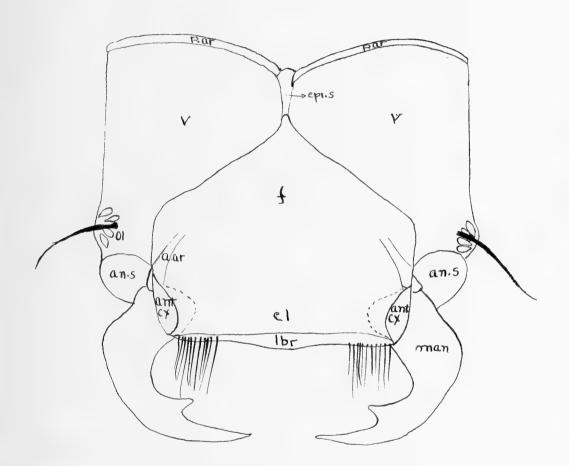




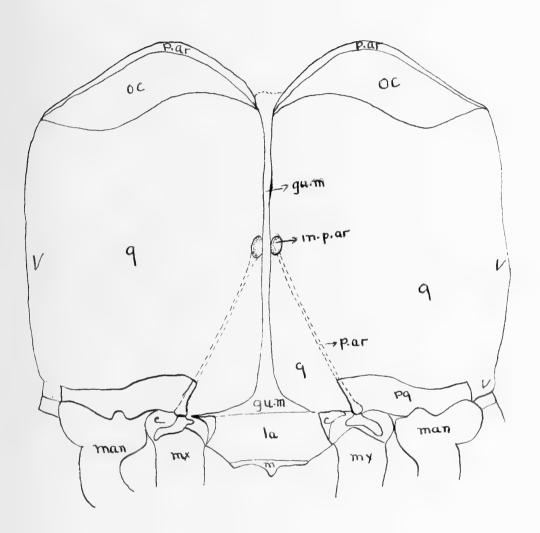




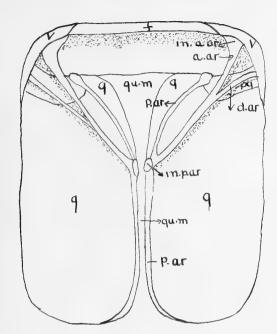










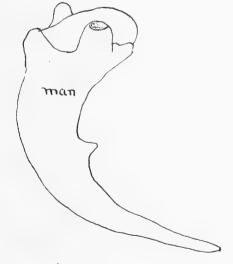


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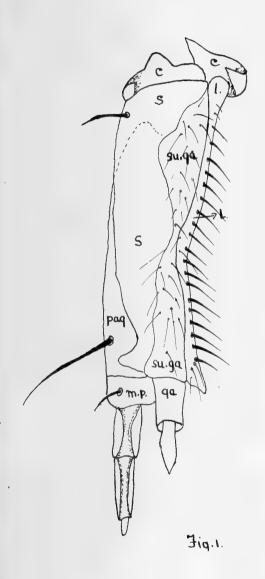
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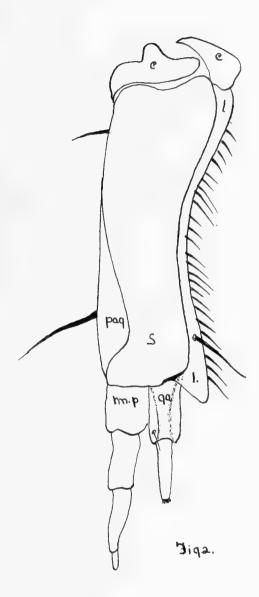




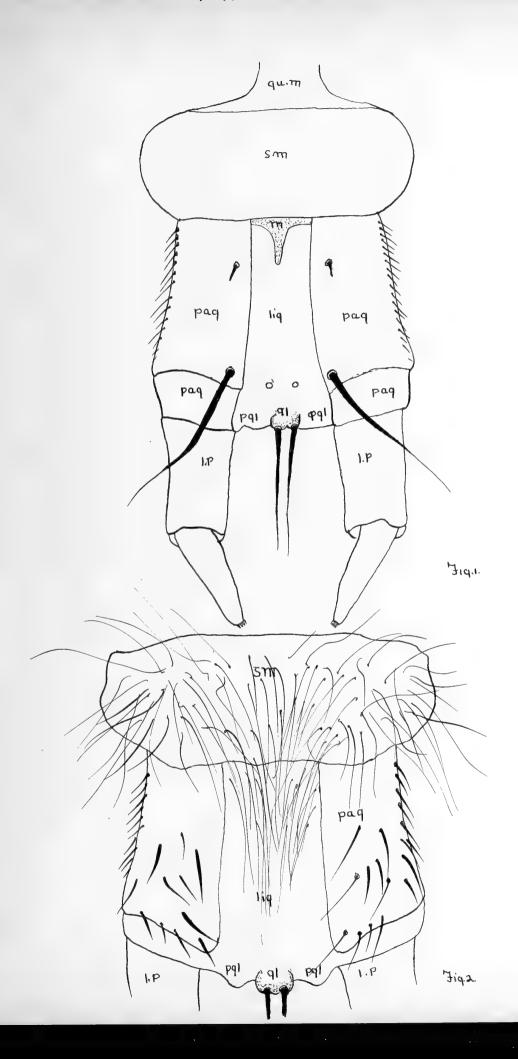
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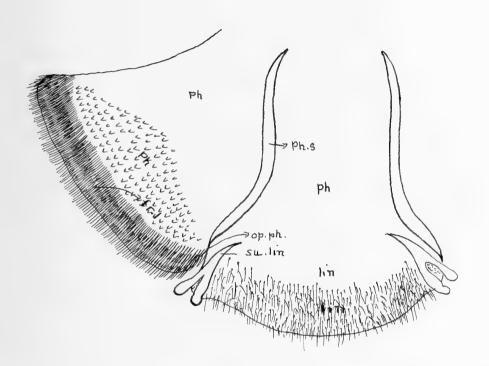




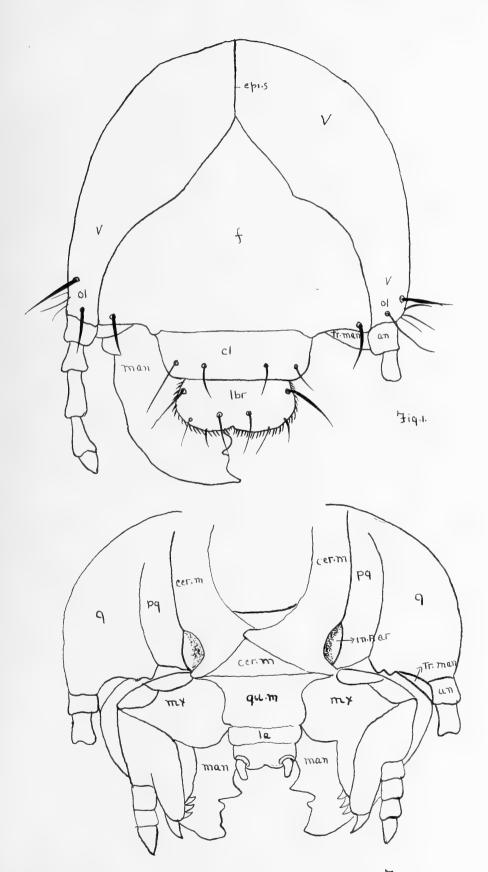






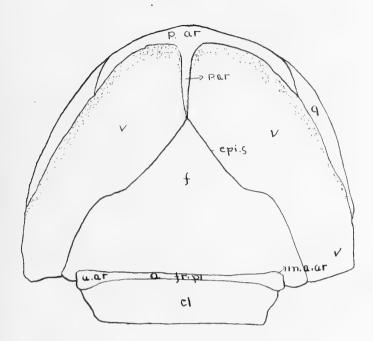




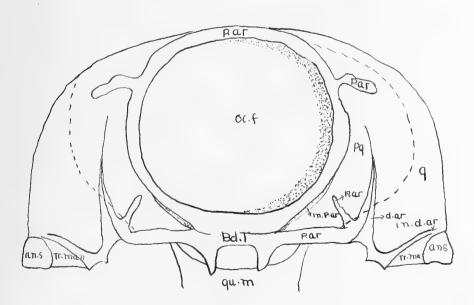


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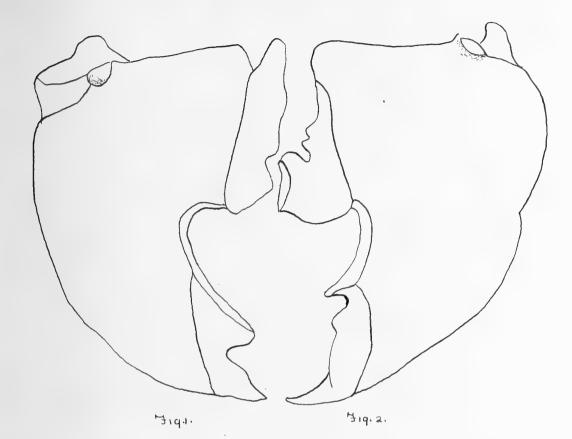


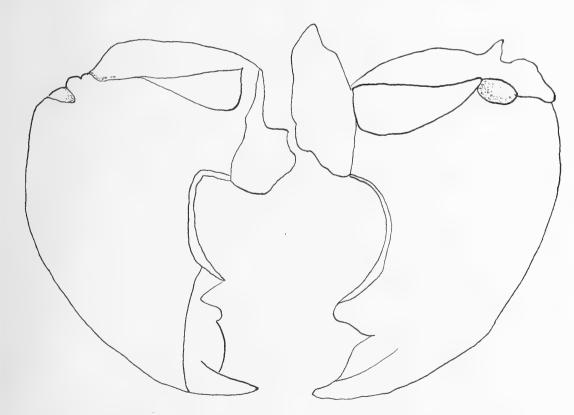
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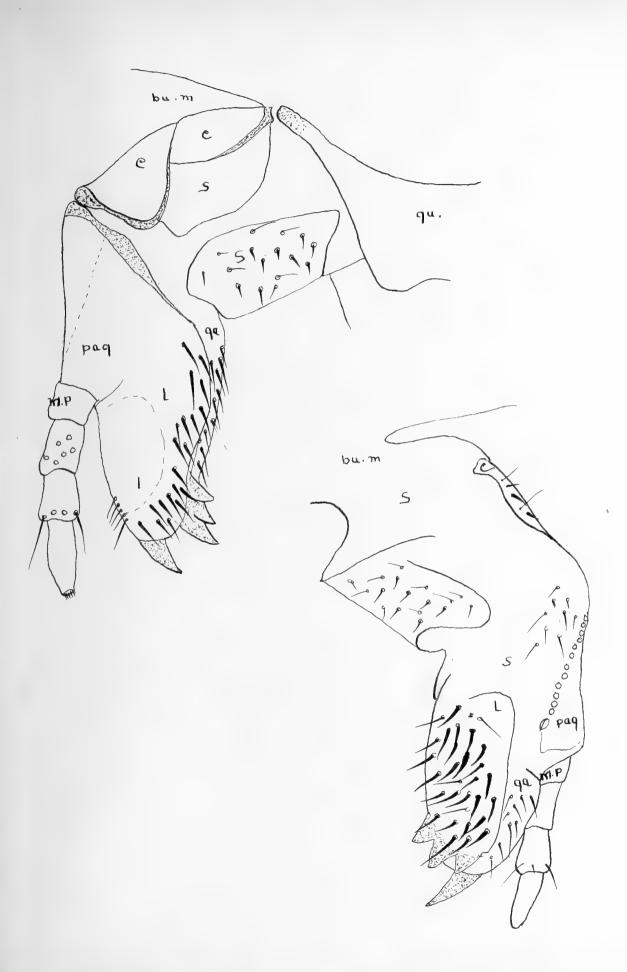




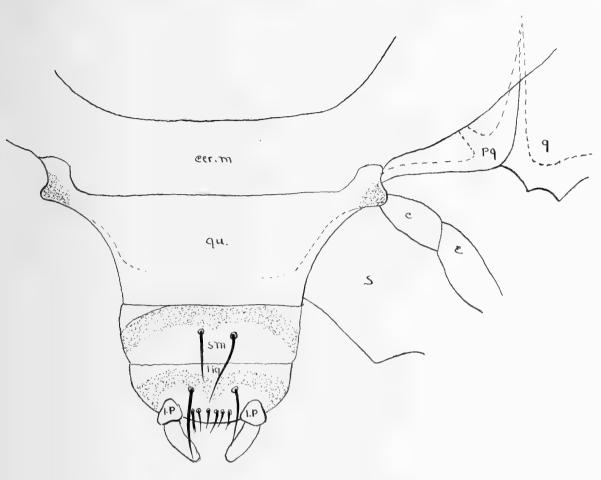
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Fig. 4.

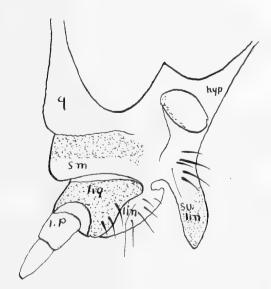






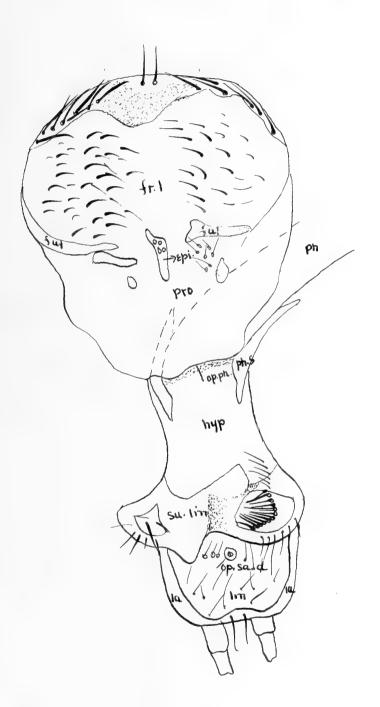


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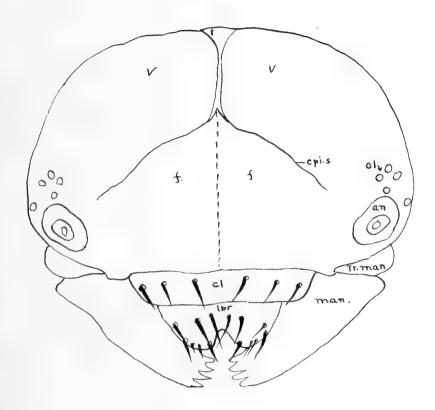


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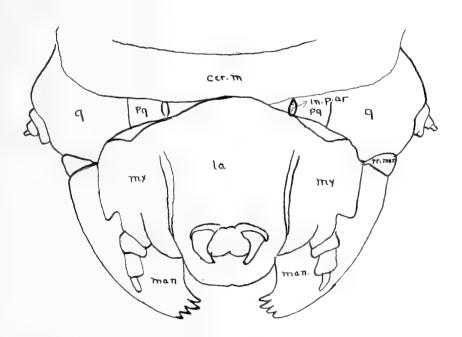






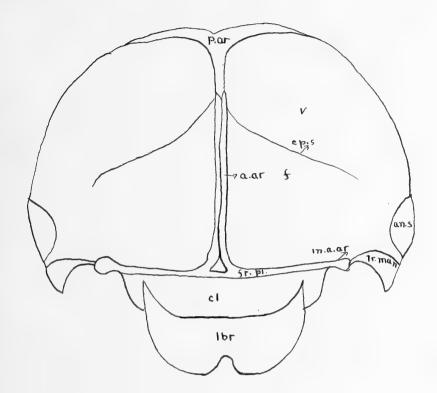


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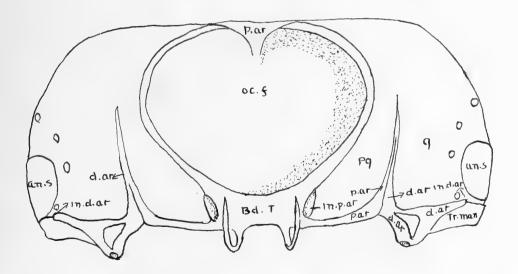


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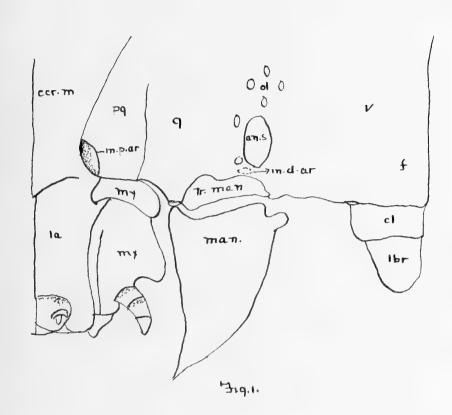


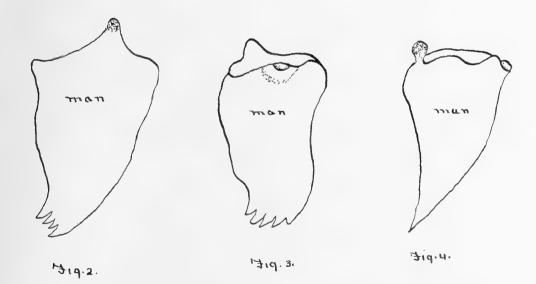
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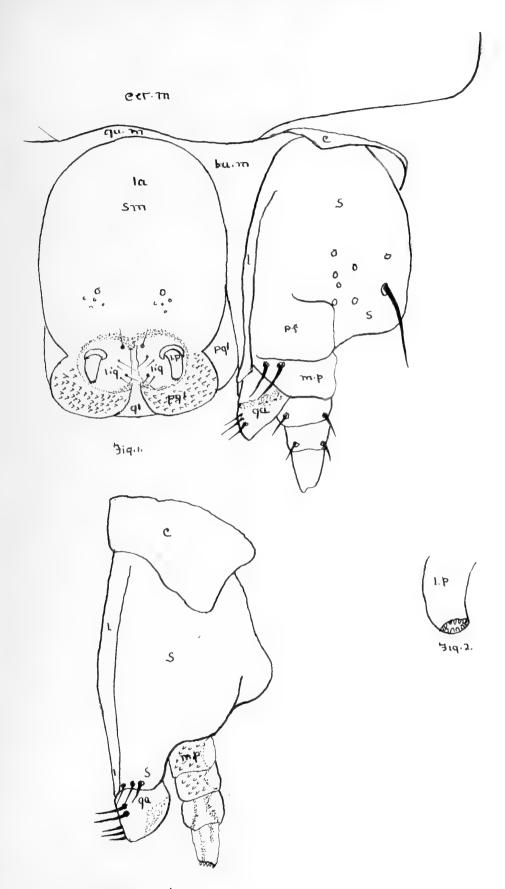
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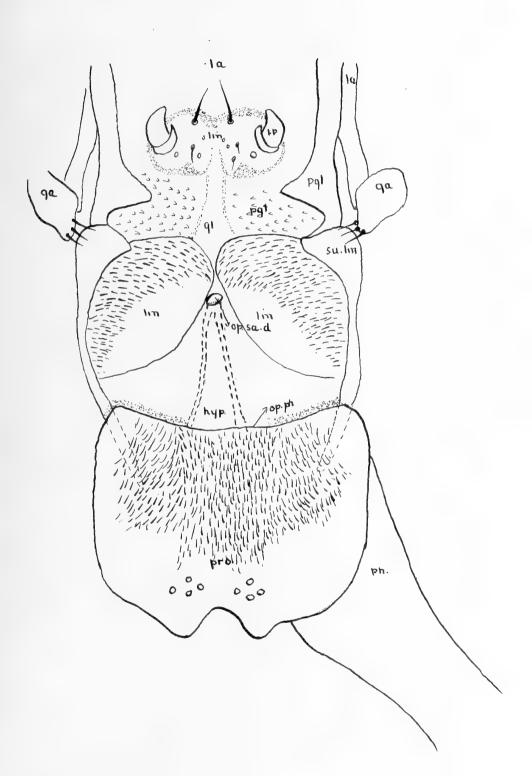




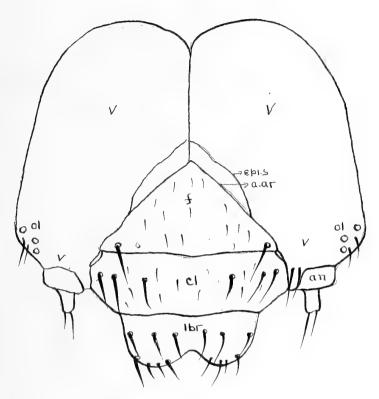


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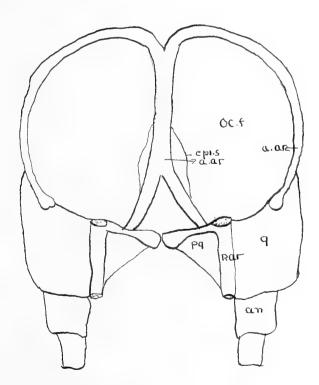






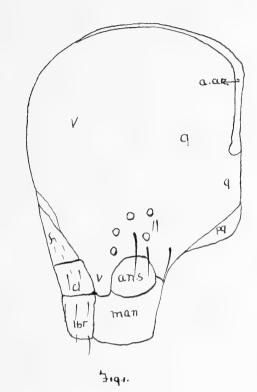


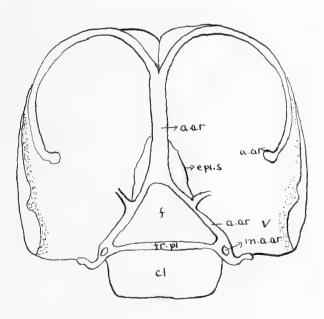
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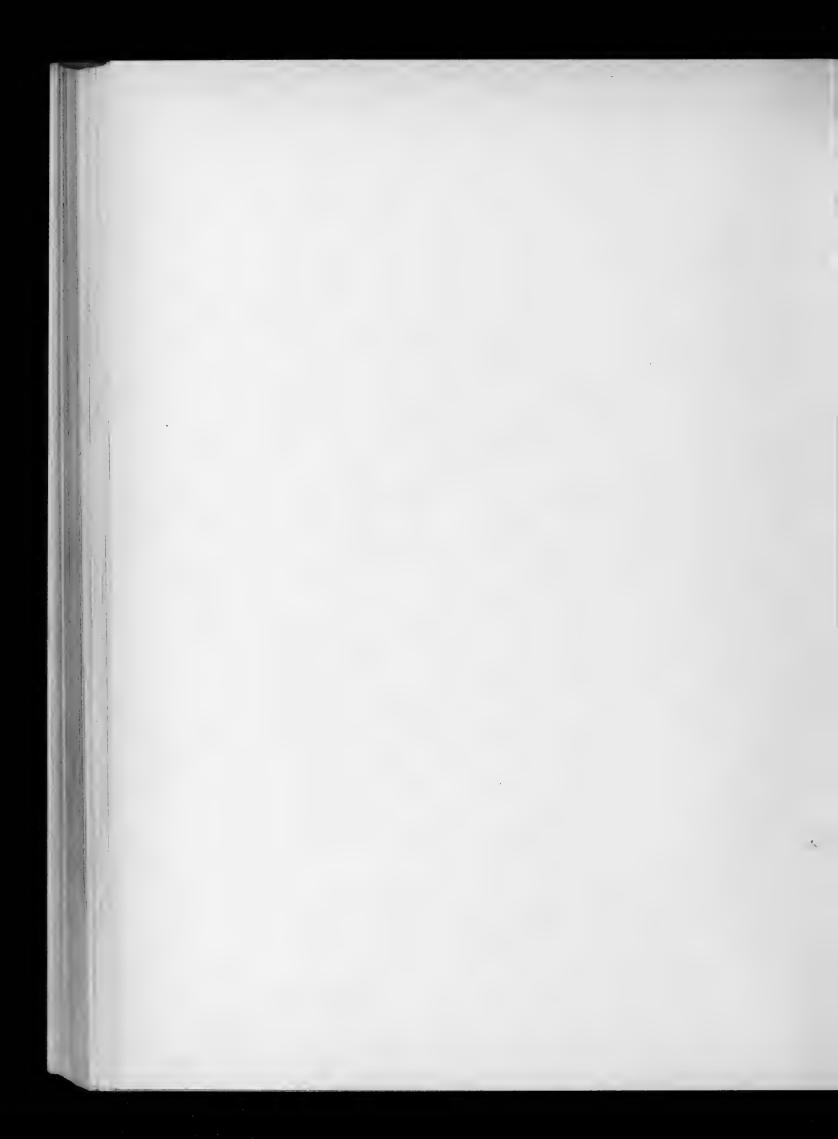
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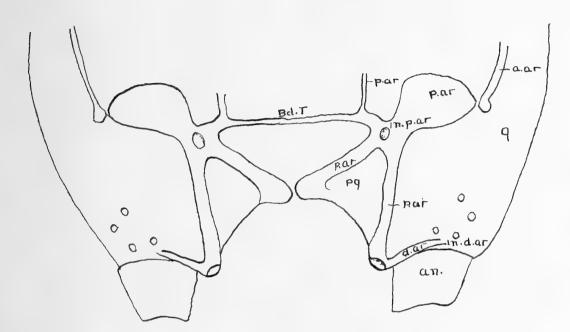




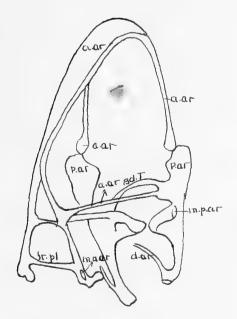


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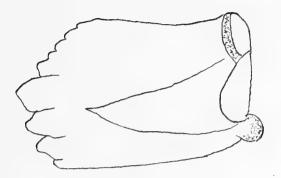


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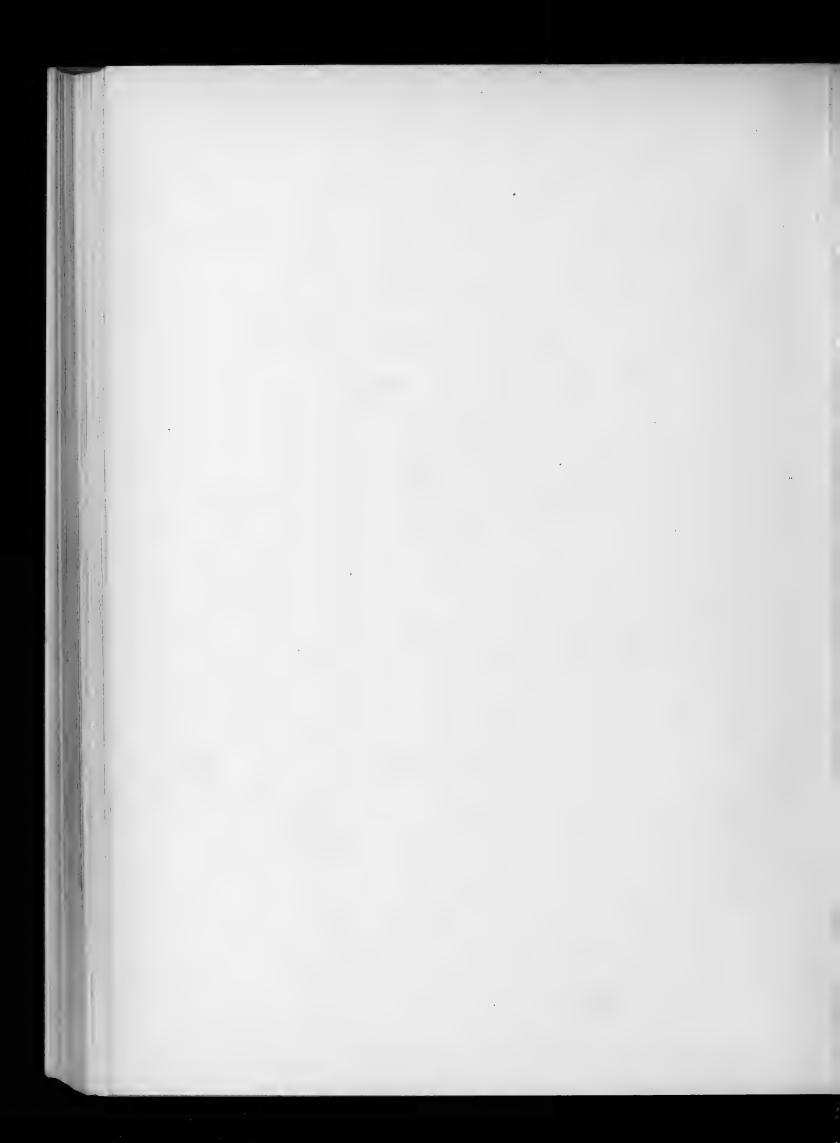


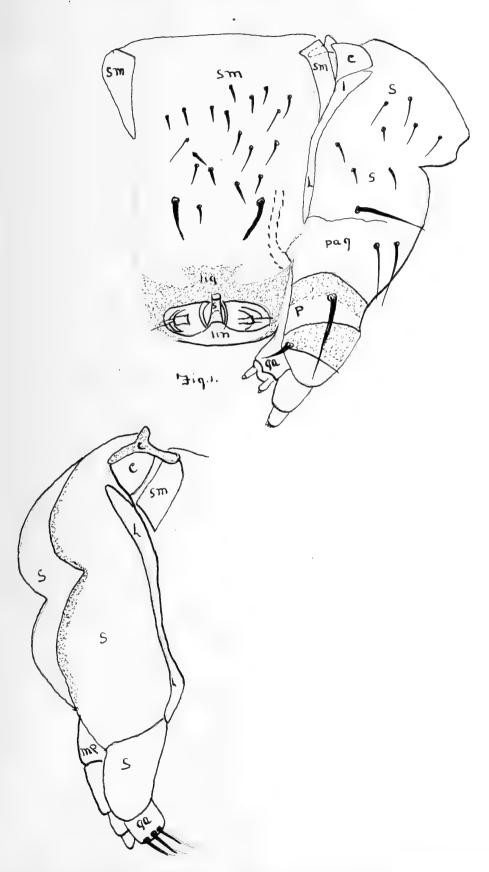
719.2.











Mig 2



